EFFECTS OF THERMAL STRESS ON SURVIVORSHIP OF BROOK TROUT (*SALVELINUS FONTINALIS*) IN ADIRONDACK LAKES

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ABSTRACT

Brook trout (*Salvelinus fontinalis*) are common in waters ranging from the Appalachian Mountains to the Arctic Circle. These popular, coldwater sport fish face an uncertain fate in light of several climate change scenarios. Assessing the potential influence of variable temperature on brook trout populations poses an important challenge to fisheries biologists. I conducted a robust design mark-recapture study in three lakes in New York's Adirondack Park to estimate population parameters related to survival, abundance, detection probability and movement under contrasting thermal conditions. Results from candidate model set comparisons support the hypotheses that brook trout living in unstratified lakes experienced reduced survivorship in hot, dry years, while fish living in nearby, stratified lakes did not. Furthermore, chronic thermal stress metrics, when added as covariates, received significantly more support in the model set than acute metrics, (i.e., maximum water temperature), highlighting the relative importance of cumulative thermal stress on adult survival.

BIOGRAPHICAL SKETCH

Newell Thomas (Tom) Daniel became interested in aquatic ecology at an early age through science-based summer camps and by catching crayfish in the local creeks near his childhood home in Alexandria, Virginia. After graduating with an associate's degree in Environmental Science from Tyler Junior College (Tyler, TX), he transferred to Cornell University and earned his bachelor's degree in Natural Resources in 2011. After graduation, Tom worked as a fisheries technician under Dr. Mark Bain, and later as a research aide for Cornell's Adirondack Fisheries Research Program under the supervision of Dr. Cliff Kraft. He is currently working towards his master's degree as Dr. Kraft's advisee. His broad research interests range from population dynamics of salmonine fishes to the landscape-scale conservation of streams, lakes, and rivers. An avid angler, you will often find Tom near the water, either catching fish or simply scanning the stream bank for interesting rocks and native mussel shells.

For Elizabeth

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CHAPTER 1

Introduction

Water temperature is a key factor influencing the population dynamics of freshwater fish (Fry 1971, Magnuson et al. 1990, Letcher et al. 2015) and as poikilotherms, fish are particularly vulnerable to warming climatic trends (Ficke et al. 2007, Eby et al. 2014). Climate change models predict increased variability of both air temperature and precipitation (Intergovernmental Panel on Climate Change 2015), both of which will influence thermal habitat conditions in aquatic ecosystems. Therefore, predicting the suitability of future thermal habitat conditions for freshwater fish will be important to understand how these organisms will respond to thermal stress associated with changing climate conditions.

Organisms adapted to cold climates are expected to shift along latitudinal and elevational gradients as the climate warms (Parmesan and Yohe 2003), and modeling approaches have been used to predict declines and range shifts in fish populations (Flebbe et al. 2006). However, few empirical studies have documented range shifts or changes in fish population dynamics in response to variable thermal conditions in lakes and streams. One notable exception was a recent study documenting a shift in bull trout distribution (*Salvelinus confluentus*) toward higher elevations in a western U.S. watershed that was associated with warming temperature conditions (Eby et al. 2014). In contrast, Magnuson et al. (1990) predicted that increasing water temperatures would result in increased thermally suitable habitat for cold-water fishes in Lake Michigan. Overall, the impacts of water temperature increases are likely to vary considerably between species and systems depending on the heterogeneity of thermal conditions and fish

physiology, therefore more empirical evaluations of the response of fish populations to variable temperature conditions are needed.

Brook trout (*Salvelinus fontinalis*) is a popular sport fish native to eastern North America that inhabits cold-water habitats from mountain streams in Georgia to boreal streams and lakes of northeastern Canada. The seasonal, spatial and geographical heterogeneity of thermal habitat conditions in lakes and streams inhabited by brook trout provide a good template for evaluating the influence of variable temperature conditions on this organism. Like other salmonine fishes, brook trout need cold water to survive (McCormick et al. 1972, Robinson et al. 2010, Xu et al. 2010). In aquatic systems where temperatures approach upper thermal limits, brook trout persist by utilizing cold-water refugia during the warm summer months (Dolloff et al. 1994, Biro 1998). These refugia are typically available at locations of upwelling groundwater along stream and lake shorelines. In addition, lentic brook trout populations often find ample thermal refuge within oxygenated hypolimnia in deep, stratified lakes.

The negative impacts of thermal stress on salmonids are well-documented (Fry et al. 1946, Xu et al. 2010, Warren et al. 2012, Letcher et al. 2015). Water temperatures above 20˚C are associated with delayed spawning (Warren et al. 2012), reduced growth (Fry 1971, McCormick et al. 1972), and increased mortality in brook trout (McCormick et al. 1972, Biro et al. 2007, Robinson et al. 2010). Impacts from thermal stress vary considerably between species and within populations for a given species, as has been specifically shown for a population of stream-dwelling brook trout (Xu et al. 2010). Additionally, individuals within a population of salmonine fishes (even within the same year class) may be more or less susceptible to warmer water temperatures depending on physiological differences (e.g., size) (Cairns et al. 2005, Letcher and Horton 2008).

The presence of cold-water refugia in lakes can mitigate some of the effects of warm temperature conditions on salmonine fishes. However, the efficacy of any single refuge depends on a host of other factors including but not limited to: the size and location of the refuge, food availability, oxygen availability and the size and age structure of the population using the refuge (Biro 1998). For example, locations of cold groundwater inputs along lake shorelines can offer some thermal protection to juvenile fish, while older fish are too large to take advantage of the microhabitat (Biro 1998). In lakes and streams that offer little or no thermal refuge, high mortality may occur when temperatures exceed the maximum thermal tolerance threshold (Robinson et al. 2010).

Abundance estimators

A challenge faced by many researchers in evaluating the relationship between environmental factors, such as temperature, on survival or abundance of fishes often stems from difficulties in estimating those population parameters. Traditional assessment methods have employed catch per unit effort (CPUE) to estimate relative changes in fish abundance. However, despite the widespread use of this metric by managers and researchers, changes in CPUE may not accurately reflect changes in true abundance (Van Oosten et al. 1946, Beverton and Holt 1993). The most basic model for the relationship between CPUE and metrics of abundance *N* is given by

$$\mathrm{CPUE}_t = q N_t$$

where *q* is the catchability coefficient. Variability in catchability can greatly influence stock assessments, which has been the focus of extensive research (Hamley 1975, Rudstam et al. 1984, Willis et al. 1985, Richards and Schnute 1986). Adding to this uncertainty, the relationship

between CPUE and *N* has been shown to be non-linear in some cases (i.e., declines in abundance may not be reflected by declining catch rates) (Ricker 1940, Kraft and Johnson 1992, Harley et al. 2001). Nevertheless, CPUE continues to be used as a proxy for abundance when more time intensive methods, such as capture-mark-recapture (CMR) studies, may not be feasible or cost effective (Jessup and Millar 2011, Koenig et al. 2015).

Recent studies have focused on identifying sources of error in the CPUE-abundance relationship (McInerny and Cross 2006, Ward et al. 2012, Peterson et al. 2015). In comparisons of catch rates estimated from multiple gear types to estimates obtained through CMR techniques, some researchers have identified instances where CPUE fails to predict relative abundance. For example, McInerny & Cross (2006) found seasonal and size dependent variation in catchability of black crappies (*Pomoxis nigromaculatus*), which would lead to misleading estimates of the population density. Peterson et al. (2015) demonstrated that failing to account for variability in catchability can lead to systematic biases in population estimates resulting in substantial underestimates of abundance (up to 100%). Therefore, sampling approaches that allow for the direct estimation of detection probability are required to provide more precise population estimates (Williams 2002).

This thesis describes work designed to evaluate the effects of thermal stress on brook trout survival in stratified and unstratified Adirondack lakes that present contrasting thermal conditions in a geographic setting with similar climate and other environmental conditions. Specifically, I attempted to (i) identify the relative importance of chronic vs. acute thermal stress on brook trout survival and (ii) model the relationship between thermal stress and survival within two lake-dwelling brook trout populations under contrasting thermal regimes. I also attempted to

demonstrate how CMR data can be used to obtain precise abundance estimates while evaluating the following main hypotheses:

1. Brook trout survival declines in an unstratified lake when summer water temperatures exceed stressful temperature thresholds.
2. Survival of brook trout in a nearby, stratified lake does not decline when this lake system is subject to nearly identical climatological conditions.

Two additional hypotheses were also evaluated in order to determine the most appropriate thermal stress metrics in the study lakes:

1. Chronic thermal stress is more effective in predicting brook trout survival than acute thermal stress in an unstratified lake. Specifically, models that include cumulative degree-day metrics as covariates predict reductions in survivorship better than time-varying models or models in which survival is a function of maximum mean daily water temperature.
2. Based on the research by Robinson et al. (Robinson et al. 2010) and Chadwick et al. (Chadwick et al. 2015), I expect that a specific cumulative thermal degree-day metric can be used to predict brook trout survival in a lake ecosystem.

Methods

Study area

This study was conducted on two small, natural lakes located on private land holdings near Old Forge, NY in New York's Adirondack Park. Panther Lake is an 18.4 hectare lake with a maximum depth of 7.0 meters. Panther Lake does not stratify in the summer and provides negligible cold-water thermal refuge for brook trout. East Lake is a 15.2 hectare lake with a maximum depth of 11.6 meters. This lake stratifies in the summer and provides an ample thermal refuge in the form of an extensive oxygenated hypolimnion. Both lakes contain naturally reproducing brook trout populations and are located 2.1 km apart at an elevation of 555 meters above sea level. While angling does occur on these lakes, reported release rates are consistently high (above 80%; AFRP unpublished data) and removal due to harvest is generally considered to be low.

Temperature

Hobo temperature loggers were deployed in each lake immediately following ice-out to record water temperatures (hourly) from mid-May to mid-October during the course of the study (2010 – 2014). Surface water temperatures were measured at depth of 0.5 meters in each lake. In Panther Lake (unstratified), a temperature logger was deployed at the deepest point in the lake. In East Lake, a temperature logger was deployed at a depth of 2.5 m to record hypolimnetic water temperature. Acute thermal stress in Panther Lake was characterized by the maximum daily mean water temperature for each year, though this metric was not applied in East Lake due to the presence of oxygenated thermal refuge habitat throughout the year. Several cumulative degree day (*DD*) metrics were calculated to represent chronic thermal stress by summing the

cumulative difference between the daily mean temperature and a specific threshold (18ºC, 19ºC, 20ºC, 21ºC, 22ºC). Cumulative degree-days over 20ºC and 21ºC (*DD>20*, *DD>21*) have both been previously correlated with increased brook trout mortality (Robinson et al. 2012, Chadwick et al 2015), so these metrics were included as environmental covariates. Full temperature and dissolved oxygen profiles were conducted in each lake at 0.5 m intervals in mid-July and mid-August using a YSI® probe.

Field sampling

Brook trout were collected according to a sampling scheme consistent with Pollock's (1982) robust design (RD), in which multiple successive trap net occasions were conducted. Brook trout were captured from East and Panther lakes from 2010 to 2014 using four Oneida Lake-style trap nets deployed in each lake immediately following ice-out in April (Figure 1.1). Each net was deployed for either three or four nights; captured fish were processed by measuring total length (mm) and weight (g) and applying a T-bar anchor tag (Floy or Hallprint) with a unique tag number to every brook trout longer than 150 mm. The nets were reset and all fish were released near the center of the lake after all four nets were tended and after all fish recovered. The trap nets were tended two more times in each lake following another three or four-day interval, and all unmarked fish over 150 mm were tagged during each subsequent sampling occasion. These successive trap net events, hereafter referred to as "secondary" sampling occasions, are collectively described as a "primary" sampling occasions by Pollock (Pollock 1982). One primary sampling occasion, each consisting of three secondary occasions, was conducted on each lake during the spring of each year according to the methods described above.

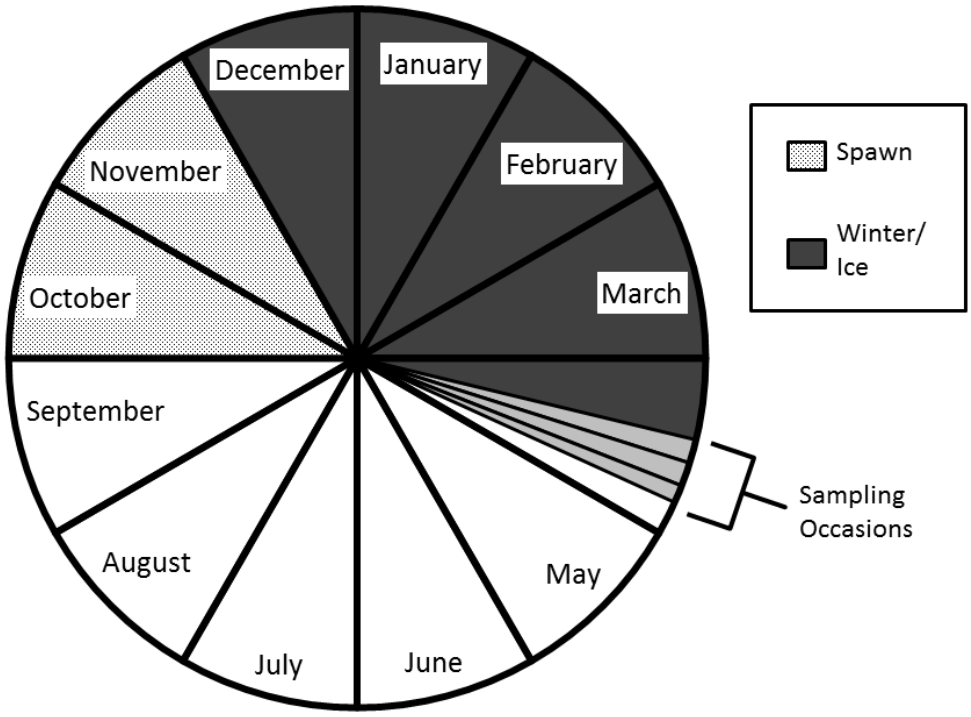

Figure 1.1. Diagram of the timing of trap net sampling occasions. Each primary occasion is composed of three secondary occasions. Sampling was conducted in the spring of each year, immediately following ice-out. Timing of spawning and winter vary from year to year.

Data analyses

I estimated annual apparent survival (*S*) and abundance ($\hat{N}$) from five years of mark-recapture data using a robust design (RD) framework (Pollock 1982, Kendall et al. 1995, Townsend et al. 2016) using Program MARK v.8.0 (White and Burnham 1999). The RD approach combines the Cormack-Jolly-Seber (CJS) parameterization, which enables the estimation of survival over an open interval, with closed capture abundance estimation (Otis et al. 1978) over a closed time interval. CJS models estimate apparent survival between primary occasions (years, in this case, from April/May in one year to April in the next). The closed capture abundance models rely on multiple secondary sampling occasions in quick succession to satisfy the "closure" assumption necessary for unbiased abundance estimation. Furthermore, the additional years of data lead to substantial gains in precision of the detection probability estimates within primary occasions, increasing precision of abundance estimates, while also enabling estimation of movement parameters (γ' and γ'') that are inestimable using the RD's constituent model types (Kendall et al. 1995, Cooch and White 2016). I developed a candidate set of approximating models using the Huggins parameterization (Huggins 1989) for the closed population abundance estimation (either alone, or embedded in the robust design), which allowed for the use of individual covariates. The parameters in the Huggins RD are:

> S_i = apparent survival probability from sampling occasion (*i)* to (*i* + 1*).* Apparent survival reflects overall subtractions from the population (true mortality + permanent emigration).
>
> γ' = probability of an individual being unavailable for capture during a primary sampling event (*i*), given that it *was not* available during the previous event (*i* – 1), *and* that it survives to time (*i*).

γ'' = probability of an individual being unavailable for capture during a primary sampling event (i), given that it *was* available during the previous event ($i - 1$), *and* that it survives to time (i).

p_i = is the probability of initial encounter, conditional on survival and being available in the sampling population at time (i).

c_i = is the probability of subsequent encounter, conditional on initial capture (p).

Huggins (1989) models allow for the incorporation of individual covariates by conditioning abundance (N) out of the likelihood equation, given that no covariate values are available for individuals that were never encountered. Under the Huggins parameterization, abundance is derived using a Horvitz-Thompson estimator:

$$\widehat{N} = \sum_{i=1}^{M_{t+1}} \frac{1}{1 - [1 - \hat{p}_1(x_1)][1 - \hat{p}_2(x_2)] \ldots [1 - \hat{p}_i(x_i)]}$$

where M_{t+1} = the number of unique individuals caught and $\hat{p}$ = the estimate of detection probability (Cooch and White 2016). The parameters for each model were obtained using maximum likelihood estimation (MLE).

Closure tests

Violations of the closure assumption may lead to substantial biases in detection probability (p) and therefore may bias other parameter estimates. However, three instances where p estimates are unaffected (i.e., are unbiased) by violations of closure were outlined by (Kendall 1999). The p estimates are minimally affected when: (i) movement in and out of the study area is completely random, (ii) all of the individuals are present at the beginning of the study period (and the later detection probabilities are pooled in the models), or (iii) all of the individuals are

present at the end of the study (and the earlier detection probabilities are pooled in the models) (Kendall 1999). I tested for closure using Pradel time-symmetric models (with recruitment) as outlined by Boulanger et al. (2002). I produced a candidate set of approximating models for each year (Table 1.1) and compared them to a model with constraints applied to the recruitment terms (which represent additions to the population, including immigration) and survival terms (which represent subtractions from the population, including emigration) terms (i.e., $f = 0$, $\varphi = 1$). Closure can be assumed if the constrained model performs as well as the top unconstrained model in the candidate set ($\Delta AICc < 2$).

Parameter estimation and identifiability

The identifiability of the parameters associated with detection probabilities (*p* and *c*) and the movement parameters (γ parameters) were assessed using a simplified Huggins closed capture abundance model set and a reduced RD model set, respectively. Extrinsically nonidentifiable parameters can lead to convergence problems during the estimation process and can lead to errors in model selection based on the AIC_c (Townsend et al. 2016). I fit a set of 13 closed capture approximating models to the data from each closed period in each lake following the structures suggested by Otis et al. (1978) using (*LENGTH*) and (*LENGTH+LENGTH^2*) as individual covariates. When simulated annealing failed to aid convergence of certain parameters in this model set, I was required to implement some constraints to aid in parameter estimation. Although these preliminary tests showed strong support for trap shyness in East Lake, the constraint of $p = c$, which represents the absence of trap effects, enabled the identifiability of the parameters associated with detection probability for all years in both lakes. Therefore, due to the lack of parameter identifiability with models that

Table 1.1. Candidate model set for testing for closure using Pradel models (with recruitment). Models include Survival (φ), detection probability (p), and recruitment (*f*) parameters. For each parameter, "*T*" represents a trend, "*t*" represents time variation, "." indicates that the parameter was held constant, and "*FIX*" indicates that the parameter was fixed.

Model Name
*φ(t) p(LENGTH*t) f(.)*
*φ(t) p(LENGTH*t) f(t)*
*φ(.) p(LENGTH*t) f(t)*
*φ(.) p(LENGTH*t) f(.)*
φ(t) p(LENGTH+t) f(.)
φ(t) p(LENGTH+t) f(t)
*φ(.) p(LENGTH*t) f(FIX 0)*
*φ(FIX 1) p(LENGTH*t) f(.)*
φ(.) p(LENGTH+t) f(.)
φ(.) p(LENGTH+t) f(t)
*φ(FIX 1) p(LENGTH*t) f(FIX 0)*
φ(.) p(LENGTH+t) f(FIX 0)
φ(.) p(.(LENGTH)) f(t)
φ(t) p(.(LENGTH)) f(.)
φ(.) p(.(LENGTH)) f(.)
φ(.) p(.(LENGTH)) f(FIX 0)
φ(.) p(.) f(t)
φ(t) p(.) f(t)
φ(.) p(t) f(.)
φ(FIX 1) p(LENGTH+t) f(FIX 0)
φ(FIX 1) p(LENGTH+t) f(.)
φ(.) p(t) f(FIX 0)
φ(FIX 1) p(t) f(.)
φ(t) p(.) f(.)
φ(.) p(T) f(.)
φ(.) p(.) f(.)
φ(FIX 1) p(t) f(FIX 0)
φ(.) p(.) f(FIX 0)
φ(.) p(T) f(FIX 0)
φ(FIX 1) p(T) f(FIX 0)
φ(FIX 1) p(T) f(.)
φ(FIX 1) p(.(LENGTH)) f(FIX 0)
φ(FIX 1) p(.(LENGTH)) f(.)
φ(FIX 1) p(.) f(FIX 0)
φ(FIX 1) p(.) f(.)

account for trap effects, the $p = c$ model structures (with and without the length covariates) were used in the subsequent analyses.

I then assessed the identifiability of the movement parameters (γ'' and γ') by fitting a set of 28 approximating models, using the $p = c$ constraint, with and without time-varying survival (*S*), following the structures proposed by Kendall et al. (1997). These included the models corresponding to "random migration" (the likelihood of becoming available for capture equals the likelihood of staying unavailable), "Markovian migration" (being available for capture is a function of the state occupied at the previous time step, *i*-1), and "no movement" (available individuals stay available and vice versa). Each scenario was modeled with and without *LENGTH* as an individual covariate. Models representing constant probabilities of availability ("dot models") were also included. The "no movement" models represent a situation where the movement parameters would tend to be unidentifiable, as the values for each parameter would be sufficiently close to the upper and lower boundaries that the values may not be properly estimated under the random or Markovian models. The no movement models proved to be the only models for which the γ parameters were identifiable for all years in both East and Panther Lakes, therefore, γ'' was fixed to zero and γ' was fixed to one (i.e., all fish were available for capture) for all subsequent analyses.

Main effects on apparent survival

In order to evaluate the potential impacts of thermal stress on survivorship, I developed an *a priori* candidate set of 73 approximating models which were fit to the data using Program MARK v.8.0 (White and Burnham 1999). The general model consisted of time-varying survival and detection probability (constrained *p = c(LENGTH + LENGTH^2)*), using the "no movement"

γ parameterization. The remainder of the model set consisted of a series of nested, reduced parameter models that were symmetrical for all main effects. I evaluated the effects of thermal stress on apparent survival by constraining *S* to be a linear function of one environmental covariate (cumulative degree day metrics [e.g., *DD>18*, *DD>19*, *DD>20*, *DD>21*, *DD>22*] or maximum water temperature (*MAXTEMP*)) combined with and without (i) individual length (*LENGTH*) and (ii) the quadratic function (*LENGTH + LENGTH^2*) (Table S.1). Mean daily winter air temperature (*WINTEMP*), measured from October 15th to May 15th for the winter preceding each primary occasion, was also included as an environmental covariate in an attempt to parse out confounding effects of overwinter mortality. Approximating models were constructed symmetrically over the entire model set such that each main effect was modeled with and without *LENGTH* and *LENGTH + LENGTH^2* as covariates for detection probabilities. As a result, nine total models included each environmental covariate. The model set was fit to the data and the models were ranked using Akaike's information criterion (AIC; Akaike 1973) adjusted for small sample size (AIC_c; Hurvich and Tsai 1989). Model averaged estimates of *S* and *N* were obtained by multiplying the Akaike weights (i.e., the likelihood that a given model most parsimoniously describes the data) by the parameter estimates given by each model (Burnham and Anderson 2002). Cumulative AIC_c weights were used to quantify the relative effect of each environmental covariate on apparent survival since the model set was balanced with respect to all main effects (Burnham and Anderson 2002, Doherty et al. 2010). The predictor variable with the largest cumulative weight was determined to be the most important factor contributing to annual survival. Conversely, the predictor variable with the smallest cumulative AIC_c weight was deemed to be least important.

Results

Temperature

Cumulative degree-day metrics reached their maxima during the summer of 2012 in the unstratified lake (Panther Lake) with a *DD>20* value of 185.6 (Table 1.2) indicating that a major thermal stress event occurred in 2012. Mean daily water temperatures at the bottom of Panther Lake reached or exceeded 23°C for 35 consecutive days, from July 11 to August 14, reaching the peak temperature of 24.1^{o}C on August 6, 2012 (Figure 1.2). By contrast, water temperatures in Panther Lake never exceeded 21^{o}C during the relatively cool summers of 2011 and 2013, with *DD>20* values of 4.9 and 4.8, respectively. The stratified lake (East Lake) provided a thermal refuge throughout the study as indicated by the hypolimnion temperature loggers. These data were confirmed by temperature profiles that recorded bottom temperatures of 5.5^{o}C in late July 2012 (Figure 1.3).

Field sampling

A total of 1750 fish in Panther Lake were tagged over the course of the five-year study (Table 1.3). Catch rates remained relatively high in the first three years of the study, during which mean CPUE was 18.0 fish/trap net night. In the final two years of the study, CPUE declined substantially to 2.8 fish/trap net night in 2013 and 2.5 fish/trap net night in 2014 (Figure 1.4). Overall, 1793 fish were tagged in East Lake from 2010 to 2014. Spring trap net CPUE in East Lake showed considerable annual variability, ranging from 27.6 fish/trap net night in 2010 to 6.5 fish/trap net night in 2012 (Figure 1.5, Figure 1.6).

Table 1.2. Cumulative degree-day metrics and maximum temperatures taken from water temperatures at the bottom of Panther Lake from 2010 to 2014.

Year	DD > 18°C	DD > 19°C	DD > 20°C	DD > 21°C	DD > 22°C	Max Temp (°C)
2010	181.6	108.9	49.5	17.4	0	22.0
2011	69.9	27.8	4.9	0	0	20.6
2012	344.9	261.0	185.6	115.0	59.5	24.1
2013	79.7	35.0	4.8	0	0	20.8
2014	76.9	28.9	2.9	0	0	20.5

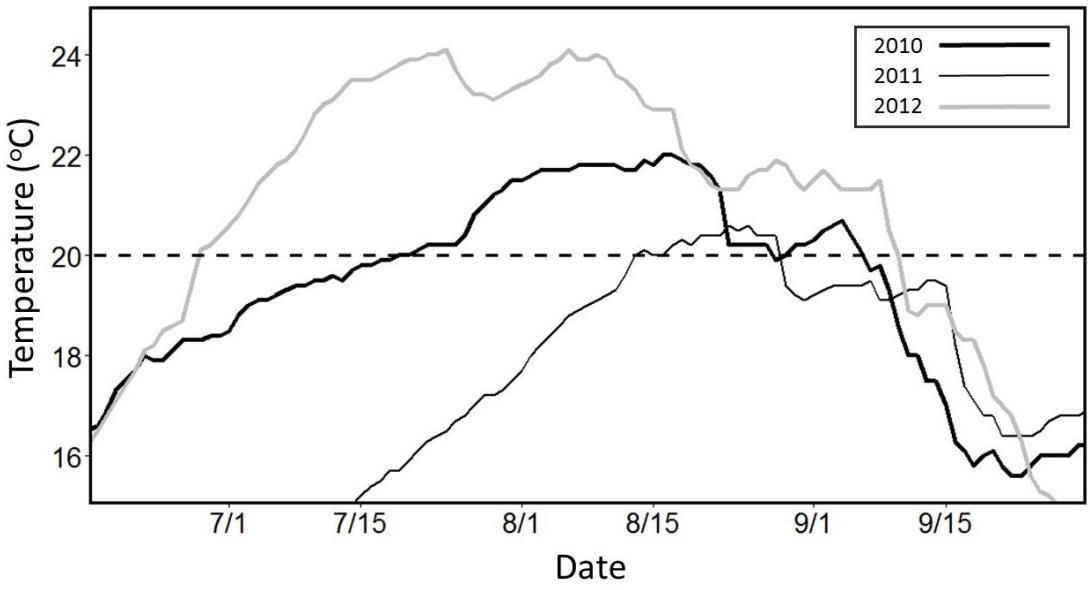

Figure 2.2. Maximum water temperatures (based on daily means) at the bottom of Panther Lake from 2010 to 2012. Thermal condition in 2013 and 2014 were similar to 2011 and were omitted from this figure for simplicity.

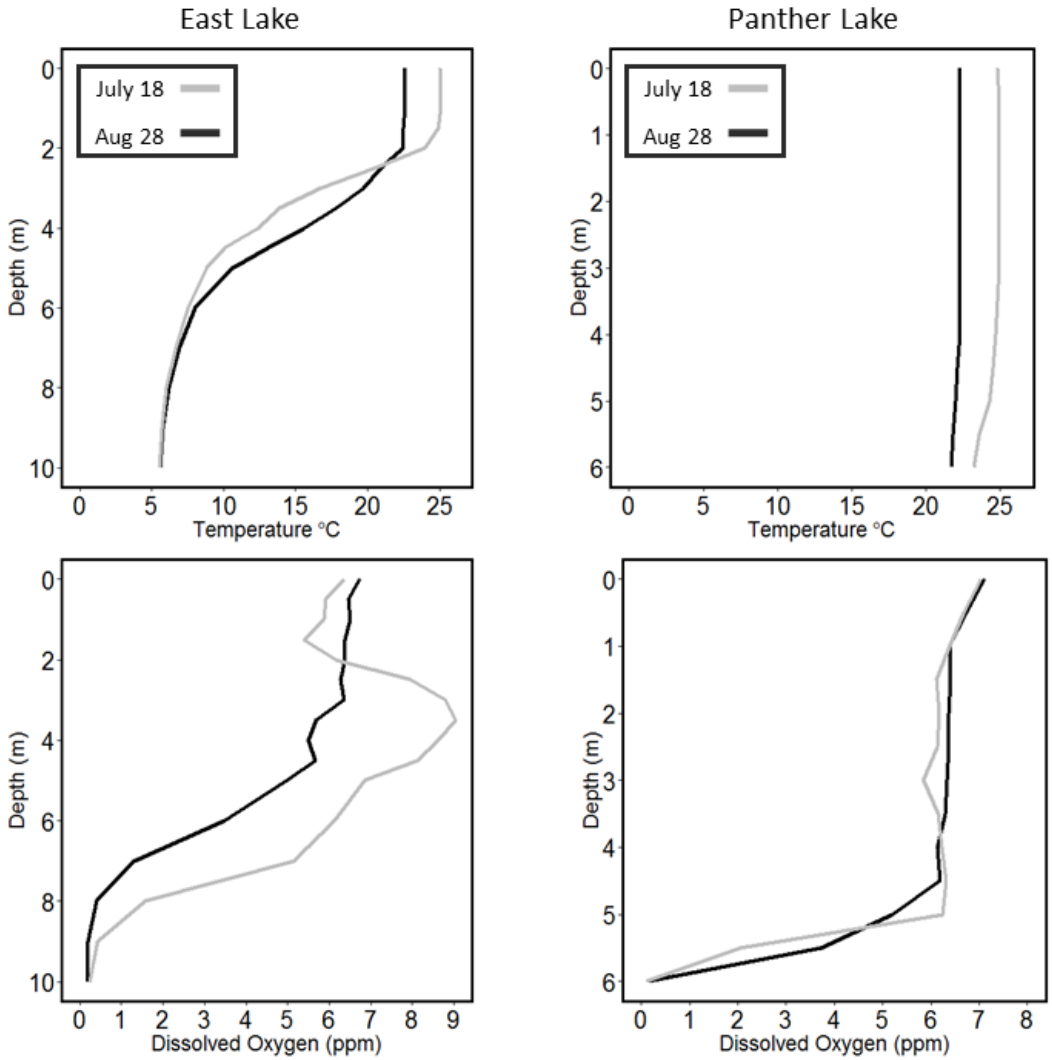

Figure 1.3. Temperature and dissolved oxygen profiles from East Lake and Panther Lake from the summer of 2012.

Table 1.3. Initial captures and recaptures from East and Panther Lakes for spring trap net samples (all secondary occasions combined). The number of newly tagged fish plus individuals recaptured at least once (i.e., # of unique tags recorded) is represented by M_{t+1}.

	Year	Tags Applied	Recaptures	Total	M_{t+1}
East Lake					
	2010	692	306	998	739
	2011	237	157	394	343
	2012	156	97	253	212
	2013	359	125	484	394
	2014	293	158	451	369
Panther Lake					
	2010	680	95	775	705
	2011	384	85	469	453
	2012	496	249	745	646

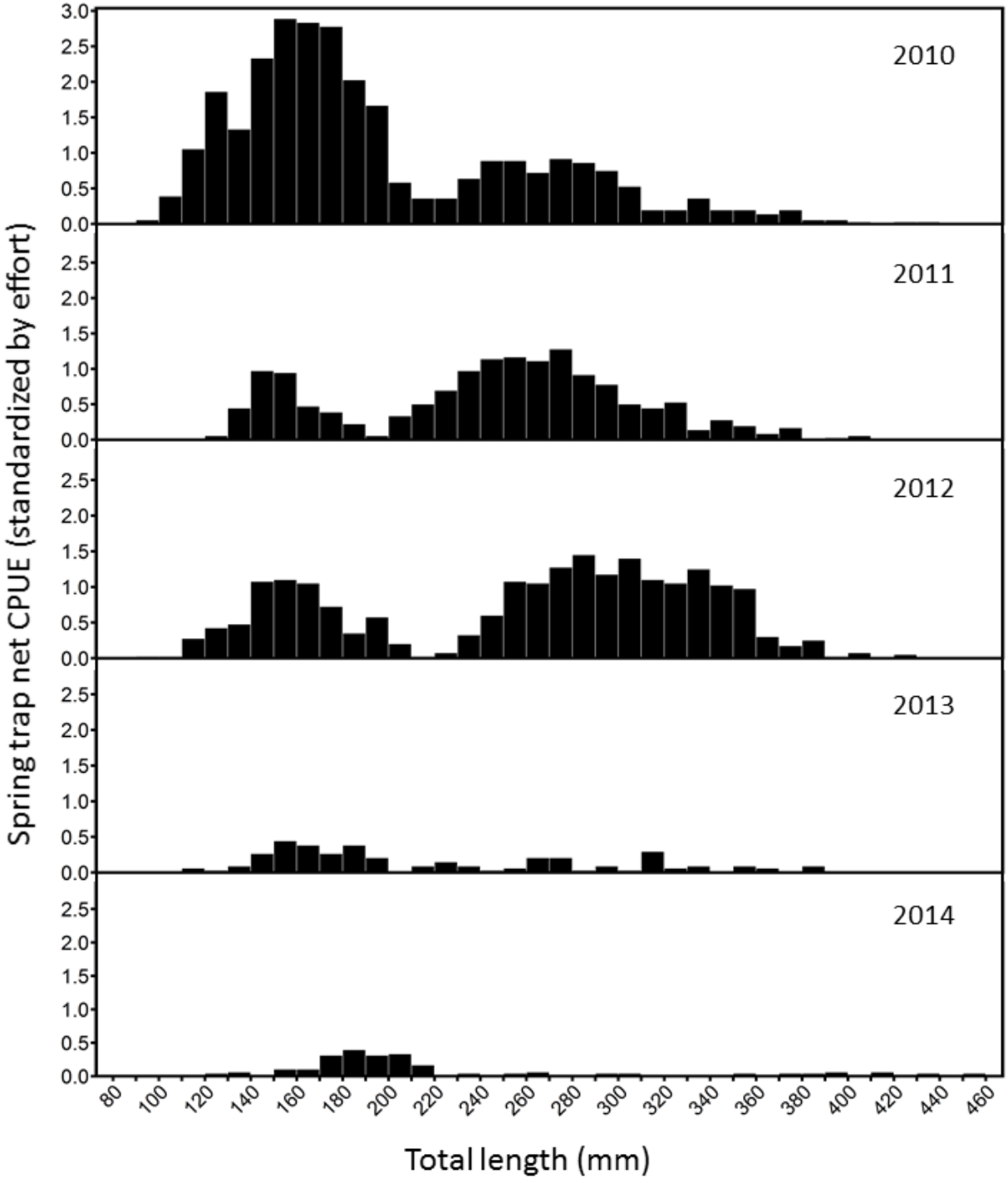

Figure 1.4. Length frequency histogram of the spring trap net catch from 2010 to 2014 in Panther Lake, standardized by effort.

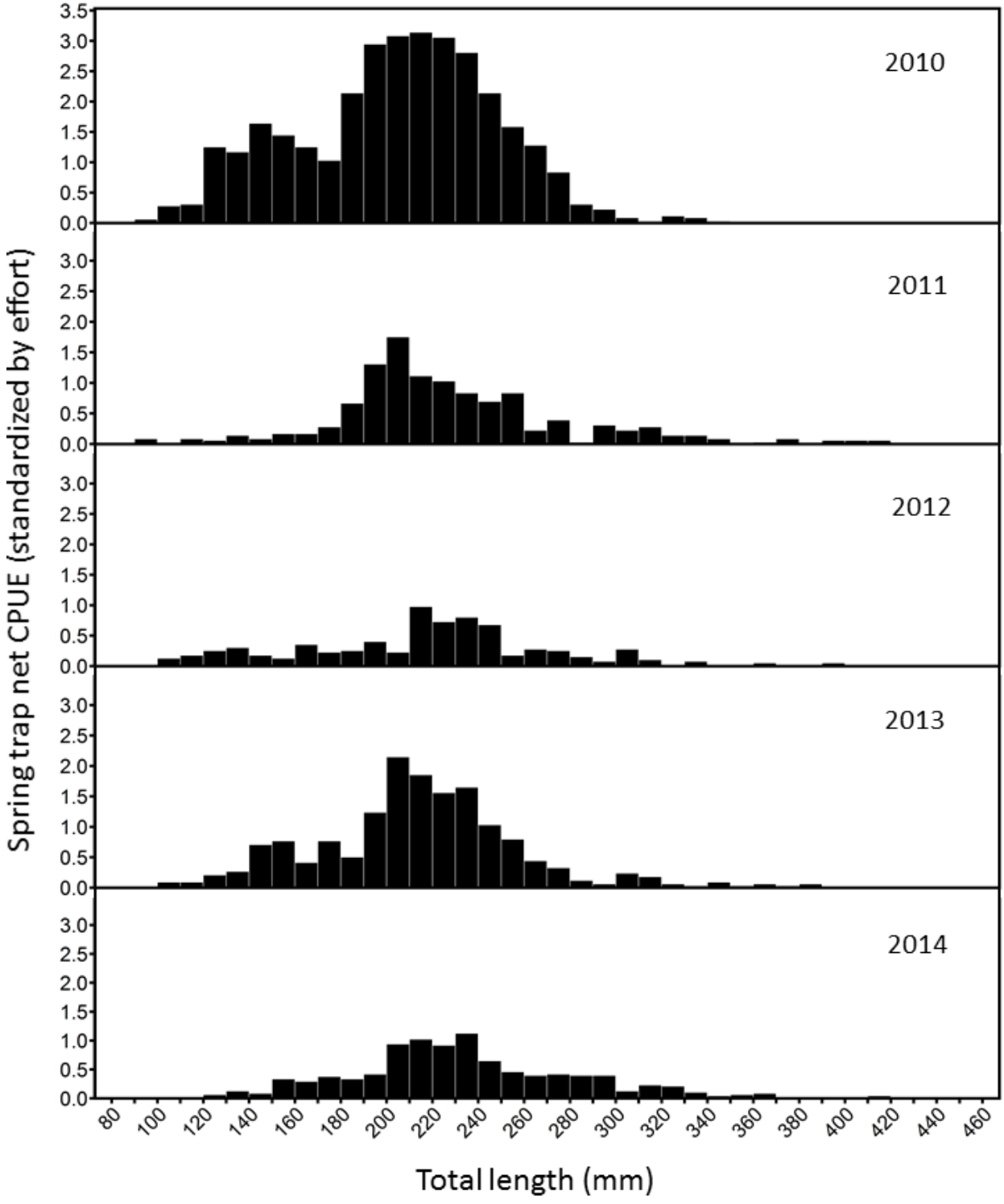

Figure 1.5. Length frequency histogram of the spring trap net catch from 2010 to 2014 in East Lake, standardized by effort.

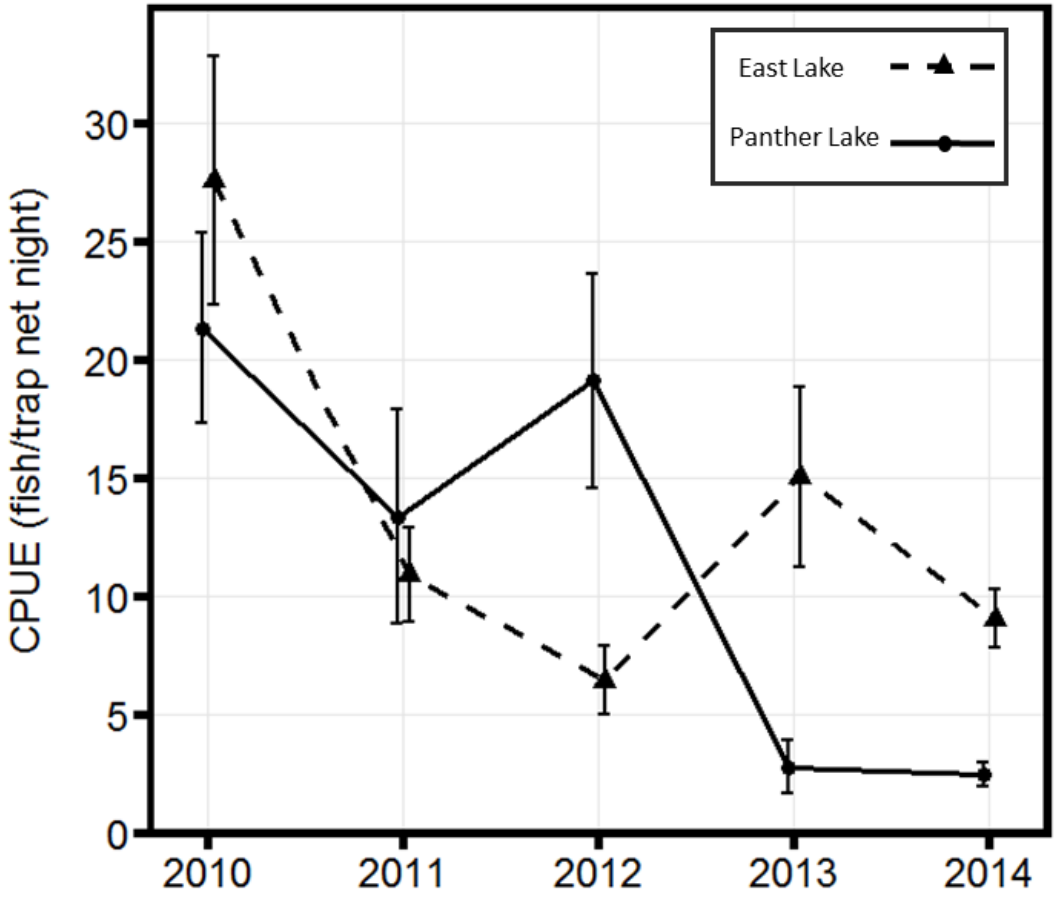

Figure 1.6. Plot of spring trap net CPUE for East and Panther Lakes, standardized by effort.

Closed capture

The Huggins closed capture models, implemented for each individual year for each lake, yielded mixed results. For Panther Lake, all models accounting for trap effects – where initial encounter probability (p) was estimated separately from subsequent encounter probability (c) – failed to converge on values for p for all years in the study. Data cloning, simulated annealing and constraining the parameters to be a function of (*LENGTH*) did not facilitate numerical convergence. In the case where time invariant models, though not well supported, did enable the separate estimation of p and c, the parameters were estimated to be similar in value. For all years in Panther Lake, $p = c$ models received overwhelming support in terms of cumulative AIC_c weights, providing strong evidence for the lack of trap effects (Table 1.4). In East Lake, models accounting for trap effects converged on parameter estimates for both p and c in each of the five years. In these cases, the estimates for initial encounter were at least double those for subsequent encounter, suggesting trap shyness (Table 1.5). Furthermore, models accounting for trap effects received 80% to 99% support in the form of cumulative AIC_c weights versus the $p = c$ models, suggesting overwhelming support for trap shyness in East Lake.

Closure test

The tests for closure using the Pradel models encountered parameter identifiability problems similar to those from the Huggins closed capture models. For all years in Panther Lake, only the models for which survival and recruitment were fixed yielded estimable parameters with the exception of 2014 (Table 1.6). Since no basis for comparison can be drawn, no inference can be made regarding the status of the closure assumption for Panther Lake. For each year in East Lake, time-invariant survival was estimable when recruitment was fixed to zero.

Table 1.4. Model selection results from the within-year closed capture models for Panther Lake.

	Model	ΔAIC_c	AIC_c weight	*K*	Likelihood
2010	$p=c(t)$	0.00	0.305	3	1.000
	$p(t(LENGTH))\ c(t(LENGTH))$	0.72	0.212	7	0.696
	$p(t)\ c(t)\ [p_i=c_i]$	1.55	0.141	4	0.461
	$p(t(LENGTH+LENGTH^2))\ c(t(LENGTH+LENGTH^2))$	1.83	0.122	9	0.401
	$p=c(t(LENGTH))$	1.87	0.120	4	0.393
	$p(Markovian)\ c(t)\ [p_i=p_{i-1}]$	3.56	0.051	5	0.169
	$p=c(t(LENGTH+LENGTH^2))$	3.71	0.048	5	0.157
2011	$p(.(LENGTH+LENGTH^2))\ c(.(LENGTH+LENGTH^2))$	0.00	0.890	6	1.000
	$p(t(LENGTH+LENGTH^2))\ c(t(LENGTH+LENGTH^2))$	5.28	0.064	9	0.071
	$p(.(LENGTH))\ c(.(LENGTH))$	6.06	0.043	4	0.048
2012	$p(t(LENGTH))\ c(t(LENGTH))$	0.00	0.716	7	1.000
	$p(.(LENGTH))\ c(.(LENGTH)$	3.31	0.137	4	0.191
	$p(t(LENGTH+LENGTH^2))\ c(t(LENGTH+LENGTH^2))$	3.51	0.124	9	0.173
	$p(.(LENGTH+LENGTH^2))\ c(.(LENGTH+LENGTH^2))$	6.86	0.023	6	0.032

Table 1.4 (cont). Model selection results from the within-year closed capture models for Panther Lake.

	Model	ΔAIC_c	AIC_c weight	*K*	Likelihood
2013	$p=c(t(LENGTH+LENGTH^2))$	0.00	0.454	5	1.000
	$p=c(t)$	1.47	0.217	3	0.479
	$p(.)\ c(.)$	3.12	0.095	2	0.210
	$p=c(t(LENGTH))$	3.14	0.094	4	0.208
	$p(Markovian)\ c(t)\ [p_i=p_{i-1}]$	3.24	0.090	4	0.197
	$p(.(LENGTH+LENGTH^2))\ c(.(LENGTH+LENGTH^2))$	5.15	0.035	6	0.076
	$p(.(LENGTH))\ c(.(LENGTH))$	6.80	0.015	4	0.033
2014	$p=c(t)$	0.00	0.317	3	1.000
	$p(Markovian)\ c(t)\ [p_i=p_{i-1}]$	0.22	0.284	4	0.897
	$p(.)\ c(.)$	1.70	0.135	2	0.427
	$p=c(t(LENGTH))$	2.01	0.116	4	0.366
	$p(.(LENGTH+LENGTH^2))\ c(.(LENGTH+LENGTH^2))$	3.32	0.060	6	0.190
	$p(.(LENGTH))\ c(.(LENGTH))$	3.85	0.046	4	0.146
	$p=c(t(LENGTH+LENGTH^2))$	4.09	0.041	5	0.129

Table 1.5. Model selection results from the within-year closed capture models for East Lake.

	Model	ΔAIC_c	AIC_c weight	*K*	Likelihood
2010	*p(t(LENGTH+LENGTH²)) c(t(LENGTH+LENGTH²))*	0.00	1.000	9	1.000
2011	*p(.(LENGTH+LENGTH²)) c(.(LENGTH+LENGTH²))*	0.00	0.809	6	1.000
	p=c(t(LENGTH+LENGTH²))	3.18	0.165	5	0.204
	p(.(LENGTH)) c(.(LENGTH))	7.91	0.016	4	0.019
2012	*p=c(t(LENGTH+LENGTH²))*	0.00	0.871	5	1.000
	p(Markovian) c(t) $[p_i=p_{i-1}]$	3.86	0.126	4	0.145
2013	*p=c(t(LENGTH+LENGTH²))*	0.00	0.871	5	1.000
	p(Markovian) c(t) $[p_i=p_{i-1}]$	3.86	0.126	4	0.145
2014	*p(.(LENGTH+LENGTH²)) c(.(LENGTH+LENGTH²))*	0.00	0.757	6	1.000
	p(.(LENGTH)) c(.(LENGTH)	2.73	0.193	4	0.255
	p(t(LENGTH+LENGTH²)) c(t(LENGTH+LENGTH²))	6.09	0.036	9	0.048

Table 1.6. Model selection results from the Pradel models with recruitment for Panther Lake. *K* = number of parameters. Each model includes Survival (φ), detection probability (p), and recruitment (*f*) parameters. For each parameter, "*T*" represents a trend, "*t*" represents time variation, "." indicates that the parameter was held constant, and "*FIX*" indicates that the parameter was fixed. Closure is represented by fixing survival to 1 and fidelity to 0.

	Model	ΔAIC_c	AIC_c weights	*K*	Likelihood
2010	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	0.00	0.684	6	1.000
	*φ(FIX 1) p(LENGTH*t) f(.)*	1.76	0.284	7	0.415
	φ(FIX 1) p(t) f(FIX 0)	7.31	0.018	3	0.026
	φ(FIX 1) p(t) f(.)	8.88	0.008	4	0.012
	φ(FIX 1) p(LENGTH+t) f(FIX 0)	9.19	0.007	4	0.010
2011	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	0.00	0.670	6	1.000
	*φ(.) p(LENGTH*t) f(FIX 0)*	1.42	0.330	7	0.493
	φ(FIX 1) p(t) f(FIX 0)	18.87	0.000	3	0.000
2012	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	0.00	0.999	6	1.000
	φ(FIX 1) p(LENGTH+t) f(FIX 0)	15.25	0.000	4	0.001
	φ(.) p(.(LENGTH)) f(FIX 0)	15.69	0.000	3	0.000
	φ(.) p(LENGTH+t) f(FIX 0)	15.69	0.000	5	0.000
2013	*φ(FIX 1) p(T) f(FIX 0)*	0.00	0.381	2	1.000
	φ(.) p(.) f(FIX 0)	1.16	0.214	2	0.561
	φ(FIX 1) p(t) f(FIX 0)	2.02	0.139	3	0.365
	φ(.) p(.(LENGTH)) f(FIX 0)	3.18	0.078	3	0.204
	φ(FIX 1) p(LENGTH+t) f(FIX 0)	3.79	0.057	4	0.151
	φ(.) p(t) f(FIX 0)	3.99	0.052	4	0.136
	φ(.) p(T) f(FIX 0)	4.19	0.047	4	0.123
	φ(.) p(LENGTH+t) f(FIX 0)	5.88	0.020	5	0.053
2014	*φ(FIX 1) p(T) f(FIX 0)*	0.00	0.305	2	1.000
	φ(FIX 1) p(t) f(FIX 0)	0.78	0.206	3	0.676
	φ(.) p(.) f(FIX 0)	1.44	0.148	2	0.487
	φ(FIX 1) p(T) f(.)	1.51	0.143	3	0.470
	φ(FIX 1) p(LENGTH+t) f(FIX 0)	2.94	0.070	4	0.230
	φ(.) p(.) f(.)	3.34	0.057	3	0.188
	φ(.) p(.(LENGTH)) f(FIX 0)	3.37	0.057	3	0.186
	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	6.28	0.013	6	0.043

Though the number of models with estimable parameters was reduced, estimates for survival (which is confounded with emigration out of the study area in these models) were estimable for some years. The notion that closure was violated, due to either mortality or emigration, received considerable support in 2010 ($\Delta AIC_c = 6.6$) and in 2013 ($\Delta AIC_c = 6.0$) and received weak support in 2011 ($\Delta AIC_c = 2.4$) (Table 1.7). In 2012 and 2014, however, support for the models representing a closed population (i.e., no mortality/emigration or recruitment/immigration) differed from the top model by <2 AIC_c, suggesting that the assumption of closure was not violated for those years. It should be noted that due to the reduced number of models for which survival was estimated, inference based on the cumulative AIC_c weights may not be appropriate (Burnham and Anderson 2002).

Effects of temperature on apparent survival

In Panther Lake (unstratified), annual apparent survival was strongly and negatively affected by thermal stress, as characterized by the degree-day metrics and maximum water temperature (*MAXTEMP*). Cumulative AIC_c weights calculated over the 73 models in the candidate model set showed overwhelming support for some temperature metrics versus the time-variant and time-invariant models. Two chronic temperature metrics (*DD>19* and *DD>20*) received the highest cumulative AIC_c weights and both were ranked much higher than the acute temperature metric represented by *MAXTEMP*. Models including *DD>19* were more than five times better supported than time-varying models with no covariates (Table 1.8). The coefficients for *DD>19* and *DD>20* were both negative, indicating that these metrics were estimated to have a negative relationship with apparent survival.

Table 1.7. Model selection results from the Pradel models with recruitment for East Lake. *K* = number of parameters. Each model includes Survival (φ), detection probability (p), and recruitment (*f*) parameters. For each parameter, "*T*" represents a trend, "*t*" represents time variation, "." indicates that the parameter was held constant, and "*FIX*" indicates that the parameter was fixed. Closure is represented by fixing survival to 1 and fidelity to 0.

	Model	ΔAIC_c	AIC_c weight	*K*	Likelihood
2010	*φ(.) p(LENGTH*t) f(FIX 0)*	0.00	0.881	7	1.000
	*φ(FIX 1) p(LENGTH*t) f(.)*	5.55	0.055	7	0.062
	φ(.) p(LENGTH+t) f(.)	5.93	0.045	6	0.052
	φ(.) p(LENGTH+t) f(t)	7.92	0.017	7	0.019
2011	*φ(.) p(.(LENGTH)) f(FIX 0)*	0.00	0.453	3	1.000
	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	2.18	0.152	6	0.336
	φ(.) p(LENGTH+t) f(FIX 0)	2.60	0.124	5	0.273
	*φ(.) p(LENGTH*t) f(FIX 0)*	3.30	0.087	7	0.192
	φ(FIX 1) p(LENGTH+t) f(FIX 0)	3.65	0.073	4	0.161
	φ(.) p(.) f(FIX 0)	5.24	0.033	2	0.073
	φ(FIX 1) p(T) f(FIX 0)	5.86	0.024	2	0.053
	φ(.) p(T) f(FIX 0)	7.27	0.012	3	0.026
	φ(FIX 1) p(t) f(FIX 0)	7.30	0.012	3	0.026
2012	*φ(FIX 1) p(T) f(FIX 0)*	0.00	0.490	2	1.000
	φ(FIX 1) p(t) f(FIX 0)	1.42	0.241	3	0.492
	φ(FIX 1) p(LENGTH+t) f(.)	2.90	0.115	4	0.235
	φ(.) p(.) f(.)	3.46	0.087	2	0.177
	φ(.) p(.(LENGTH)) f(FIX 0)	4.65	0.048	3	0.098
	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	6.54	0.019	6	0.038
2013	*φ(.) p(LENGTH+t) f(FIX 0)*	0.00	0.374	5	1.000
	*φ(.) p(LENGTH*t) f(FIX 0)*	0.26	0.328	7	0.876
	φ(.) p(t) f(FIX 0)	1.10	0.215	4	0.576
	φ(FIX 1) p(LENGTH+t) f(FIX 0)	4.09	0.048	4	0.129
	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	5.71	0.021	6	0.058
	φ(FIX 1) p(t) f(FIX 0)	6.82	0.012	3	0.033
2014	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	0.00	0.361	6	1.000
	*φ(.) p(LENGTH*t) f(FIX 0)*	0.17	0.332	7	0.919
	φ(.) p(.(LENGTH)) f(FIX 0)	0.80	0.242	3	0.670
	φ(.) p(LENGTH+t) f(FIX 0)	3.46	0.064	5	0.177

Table 1.8. Top models from the main effects RD model set for Panther Lake for AICc weights >0.010. The γ parameters were held constant and are not shown.

Model	ΔAIC_c	AIC_c weight	*K*	Likelihood
S(DD19+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	0.00	0.165	21	1.000
S(DD20+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	0.41	0.134	21	0.814
S(DD19) p=c(LENGTH+LENGTH^2)	1.49	0.078	19	0.474
S(MAXTEMP+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	1.49	0.078	21	0.474
S(DD20+LENGTH+LENGTH^2) p=c(LENGTH)	1.69	0.071	20	0.430
S(DD18+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	1.94	0.063	21	0.380
S(MAXTEMP) p=c(LENGTH+LENGTH^2)	1.97	0.061	19	0.373
S(DD18) p=c(LENGTH+LENGTH^2)	2.34	0.051	19	0.311
S(DD19+LENGTH+LENGTH2) p=c(LENGTH)	2.36	0.051	20	0.308
S(DD19+LENGTH) p=c(LENGTH+LENGTH^2)	2.84	0.040	20	0.242
S(MAXTEMP+LENGTH) p=c(LENGTH+LENGTH^2)	3.76	0.025	20	0.153
S(DD18+LENGTH) p=c(LENGTH+LENGTH^2)	4.17	0.020	20	0.124
S(MAXTEMP+LENGTH+LENGTH^2) p=c(LENGTH)	4.38	0.018	20	0.112
S(t) p=c(LENGTH+LENGTH^2)	4.43	0.018	21	0.109
S(DD20+LENGTH) p=c(LENGTH+LENGTH^2)	4.75	0.015	20	0.093
S(DD20) p=c(LENGTH+LENGTH^2)	4.83	0.015	19	0.090
S(DD18+LENGTH+LENGTH^2) p=c(LENGTH)	4.94	0.014	20	0.085
S(DD19+LENGTH) p=c(LENGTH)	4.97	0.014	19	0.083
S(DD21+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	5.26	0.012	21	0.072
S(DD21+LENGTH+LENGTH^2) p=c(LENGTH)	5.51	0.010	20	0.064
S(DD20+LENGTH) p=c(LENGTH)	5.69	0.010	19	0.058

Apparent survival in East Lake (stratified), by contrast, was unaffected by thermal stress, remaining relatively stable throughout the study period (Figure 1.7). The top 10 models had nearly equivalent cumulative AIC_c weights (Table 1.9). The top model (time-varying S) received less than 10% of the support from the data. The five next best supporting models did contain (*DD*) metrics, however, the 95% CI of each coefficient straddled zero, indicating that each metric may not be informative (i.e., had no relationship with survival). The ten best models were each within two AIC_c of the top model, suggesting that they have nearly equivalent support in the data.

Abundance

The RD abundance estimates of Panther Lake suggest a sharp decline in the available adult population of brook trout (>150 mm) between May 2012 and May 2013. The population declined from an estimated 1625 (95% CI = [1391,1932]) individuals in 2012 to an estimated 283 [184,494] individuals in 2013 (Figure 1.8). The estimated population in East Lake, by comparison, was relatively stable from 2010 to 2014, ranging from an estimate 1258 [1152,1391] individuals in 2010 to a minimum of 688 [466,1102] individuals in 2012. No substantial increasing or decreasing trend in the population could be discerned over the five-year study period based on the results from the RD approach, suggesting no relationship between thermal stress and abundance shifts in East Lake. The abundance estimates from the closed capture abundance estimates were consistently less precise and tended to be lower than those produced by the RD approach (Figure 1.9, Figure 1.10).

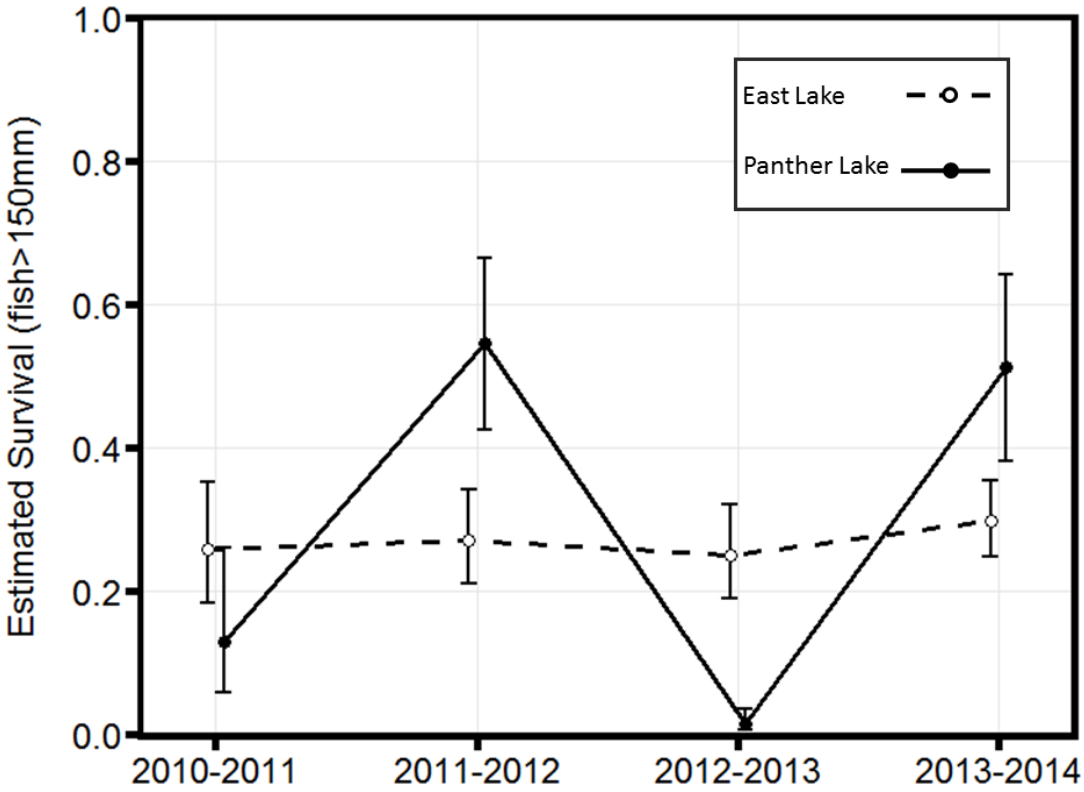

Figure 1.7. Model averaged survival estimates (*S*) from East and Panther lakes using the RD approach.

Table 1.9. Top models from the main effects RD model set for East Lake for AICc weights >0.010. The γ parameters were held constant and are not shown.

Model	ΔAIC_c	AIC_c weight	*K*	Likelihood
S(WINTEMP) p=c(LENGTH+LENGTH^2)	0.00	0.095	19	1.000
S(.) p=c(LENGTH+LENGTH^2)	0.12	0.090	17	0.943
S(DD18) p=c(LENGTH+LENGTH^2)	0.92	0.060	18	0.630
S(DD20) p=c(LENGTH+LENGTH^2)	0.94	0.059	19	0.626
S(DD21) p=c(LENGTH+LENGTH^2)	0.99	0.058	19	0.610
S(DD19) p=c(LENGTH+LENGTH^2)	1.03	0.057	19	0.596
S(DD22) p=c(LENGTH+LENGTH^2)	1.12	0.054	19	0.571
S(MAXTEMP) p=c(LENGTH+LENGTH^2)	1.13	0.054	19	0.567
S(WINTEMP+LENGTH) p=c(LENGTH+LENGTH^2)	1.18	0.053	20	0.555
S(LENGTH) p=c(LENGTH+LENGTH2)	1.51	0.045	18	0.471
S(WINTEMP+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	2.12	0.033	21	0.346
S(DD20+LENGTH) p=c(LENGTH+LENGTH^2)	2.19	0.032	20	0.335
S(DD18+LENGTH) p=c(LENGTH+LENGTH^2)	2.21	0.031	19	0.331
S(DD21+LENGTH) p=c(LENGTH+LENGTH^2)	2.23	0.031	20	0.328
S(DD19+LENGTH) p=c(LENGTH+LENGTH^2)	2.31	0.030	20	0.315
S(DD22+LENGTH) p=c(LENGTH+LENGTH^2)	2.36	0.029	20	0.308
S(LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	2.40	0.029	19	0.301
S(MAXTEMP+LENGTH) p=c(LENGTH+LENGTH^2)	2.43	0.028	20	0.297
S(t) p=c(LENGTH+LENGTH^2)	3.01	0.021	21	0.222
S(DD20+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	3.18	0.019	21	0.204
S(DD18+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	3.19	0.019	20	0.203
S(DD21+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	3.23	0.019	21	0.199
S(DD19+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	3.29	0.018	21	0.193
S(DD22+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	3.36	0.018	21	0.186
S(MAXTEMP+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)	3.40	0.017	21	0.183

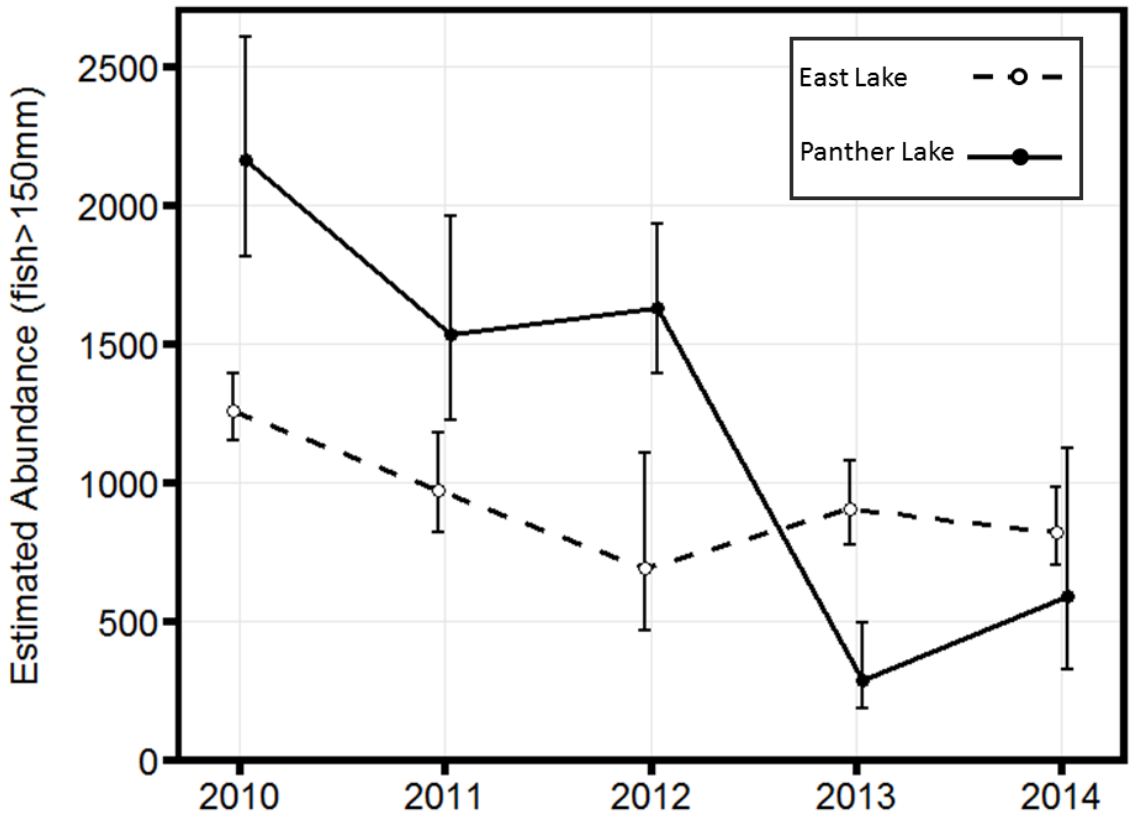

Figure 1.8. Model averaged abundance estimates of the available population of brook trout >150 mm in East and Panther lakes (RD approach).

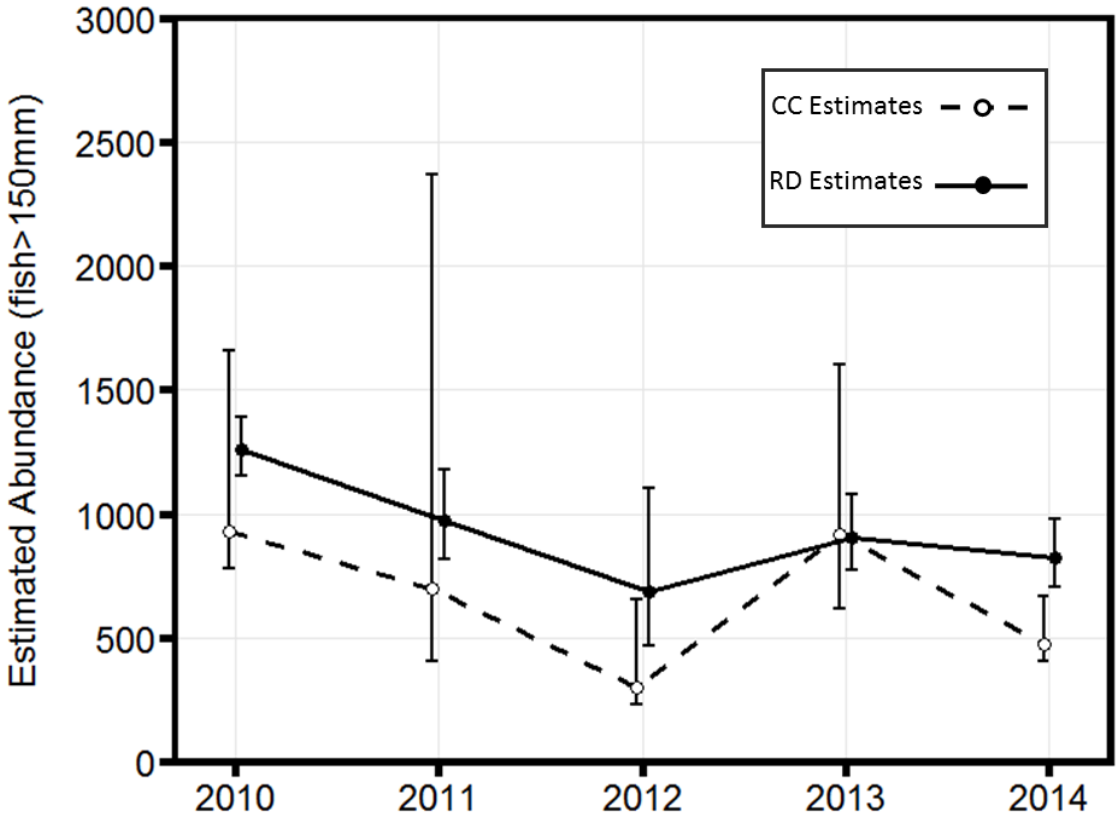

Figure 1.9. Within-year closed capture abundance estimates and those obtained from the RD approach for East Lake from 2010 to 2014.

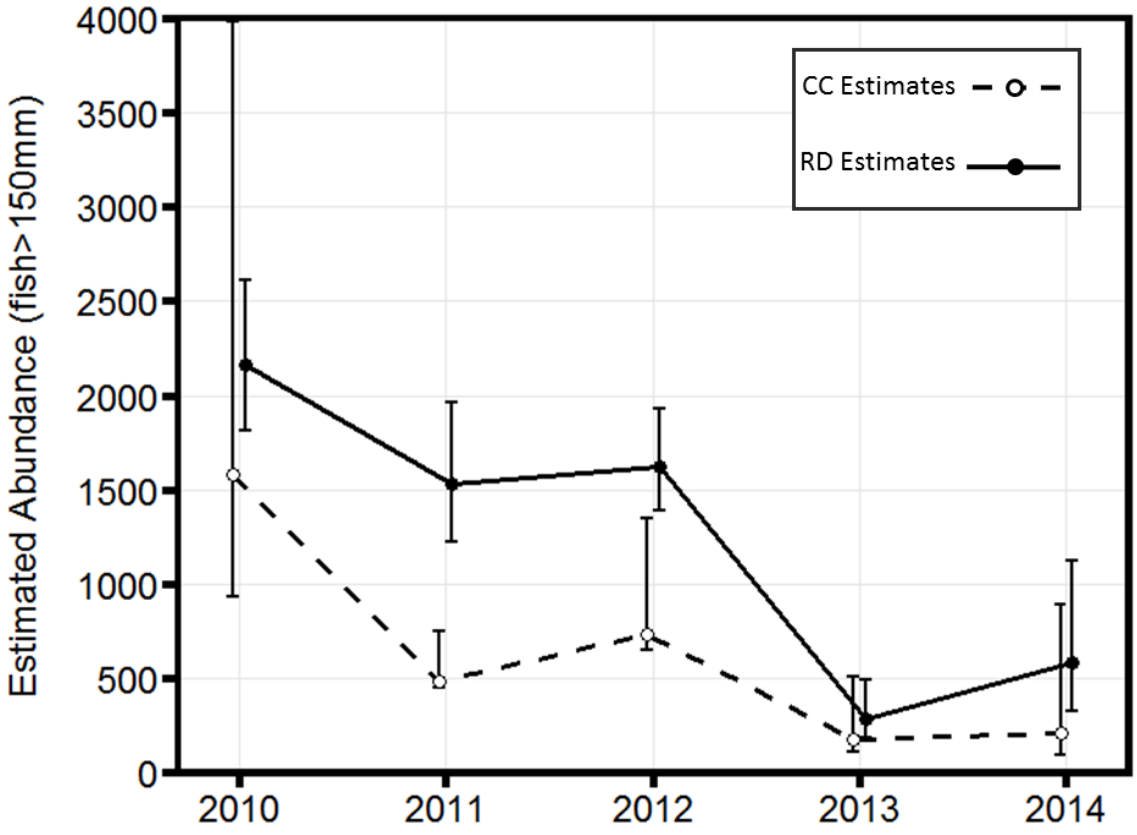

Figure 1.10. Within-year closed capture abundance estimates and those obtained from the RD approach for Panther Lake from 2010 to 2014.

Discussion

The results of this study support the hypothesis that thermal stress is associated with reduced survival of brook trout in an unstratified lake when water summer temperatures rise to chronically stressful levels. By employing a mark-recapture modeling approach, I was able to directly estimate the survival probabilities for brook trout in both study lakes while simultaneously evaluating the relative importance of chronic and acute thermal stress on brook trout survival. Furthermore, the RD approach increased the precision of abundance estimates, compared to the within-year closed capture abundance estimates, while providing some valuable insights regarding capture efficiency. During the estimation process, I discovered evidence for trap effects in detection probability, as well as evidence to support the notion that brook trout may not occupy an unavailable state in these two study lakes.

Effects of temperature on survival

Apparent survival in the unstratified lake (Panther Lake) was strongly and negatively affected by thermal stress. These results are consistent with the findings of studies that have documented temperature-induced mortality of brook trout in the laboratory (Fry et al. 1946, McCormick et al. 1972) and in another unstratified Adirondack lake prone to summer temperature conditions exceeding brook trout physiological tolerance levels (Robinson et al. 2010). Contrastingly, I found no support for increased mortality due to thermal stress in the stratified lake (East Lake) that maintained a large cold-water thermal refuge in the warmest summer (2012) during this study. These findings support our hypothesis that the presence of a hypolimnetic thermal refuge protects against reduced survivorship due to thermal stress. While this study did not attempt to test the mechanisms responsible for reduced survival under these

conditions, other studies of salmonine fishes have attributed climate-induced mortality to complex interactions between metabolism and behavior (Selong et al. 2001, Biro et al. 2007). For example, thermoregulatory behavioral responses may conflict with optimal foraging behavior, both of which play a major role in mitigating the deleterious effects of the combination of elevated cellular respiration with decreased metabolism (Wehrly et al. 2007, Goyer et al. 2014).

The study results showed that prolonged exposure to thermally stressful conditions was more closely associated with apparent brook trout mortality than acute exposure. These results support the findings of Robinson et al. (2010), in which a degree day metric (*DD>20*) was closely associated with the absence of adult year classes from trap net catches following a unusually hot summer. Chadwick et al. (2015) proposed a 21^{o}C threshold for the expression of a specific heat shock protein (HSP70); their field study did not detect this cellular stress response in streams with a 60-day mean temperature below 21^{o}C. The findings of Chadwick et al. (2015) are consistent with those described by other researchers (Meisner 1990, Wehrly et al. 2007) which support the 21^{o}C threshold. In contrast to those studies I found that a *DD>21* metric, representing a 21^{o}C threshold for prolonged exposure to thermal stress, only predicted mortality in our study system as effectively as maximum water temperature, both of which received much less support in the data than two other degree-day metrics (*DD>19* and *DD>20*). Additionally, the water temperatures at the bottom of Panther Lake reached a maximum mean daily temperature of 24.1^{o}C in the summer of 2012. Since this value is 1.3^{o}C below the upper incipient lethal temperature of 25.4 (Fry et al. 1946), long-term exposure to thermally stressful conditions is likely to have been responsible for the reduced survival observed in 2012.

Abundance

Estimated abundance of brook trout (>150 mm) in Panther Lake declined considerably between 2012 and 2013. This supports the observation that substantial mortality occurred over that time interval and is consistent with results suggesting that high summer water temperatures are associated with reduced survival. Given the overwhelming support for temperature effects on survival in the models, this observed reduction in estimated abundance is likely due to thermal stress. The abundance of brook trout in East Lake, in contrast, remained relatively stable throughout the five years of the study. The lowest estimate of 688 [466, 1102] individuals in spring 2012 was lower than the estimated abundance 902 [733, 1075] in 2013, which suggests a potential increase in abundance over the period including the hot summer of 2012, though not significant. This finding provides further support for the hypothesis that brook trout survival in East Lake would be unaffected by thermal stress during hot years.

While the data suggest that the East Lake population did not suffer any large-scale mortality events between primary sampling occasions, the population declined an estimated 35% over the five years of the study, from 1258 [1152, 1391] individuals in 2010 to 820 [981, 701] individuals in 2014. Since estimated adult survival of brook trout in East Lake remained relatively constant throughout the study period, variability in recruitment (i.e., additions to the population of brook trout >150mm) likely contributed to the estimated reduction in estimated abundance. For example, diminished spawning activity or success could reduce the number of new recruits, shrinking the future adult population even when adult survival remains constant. Additionally, reduced survival of larval or juvenile fish would have a similar effect on the future adult population without being detected using CMR techniques that only examined adult fish. This example underscores the need for caution when interpreting survival rates as an indicator of

the overall trajectory of population growth (or decline) – other parameters must also be estimated to allow for a more complete assessment.

Parameter interpretation

This study provided an opportunity to evaluate CMR data using three distinct model types, thereby allowing a comparison of modeling approaches. The Pradel (1996) models were used to test for closure, closed capture abundance estimation models were utilized in a preliminary analysis, and the RD models were fit to the data to test hypotheses and to produce robust estimates of apparent survival and abundance. Each model type requires an understanding of what the model parameters represent in order to facilitate interpretation of the estimates and the biological significance of the relative support for each model. For example, estimates of apparent survival in the Pradel models include the probability of temporary emigration, while the RD estimates of apparent survival do not. This is because the structure of the RD sampling design allows for the direct estimation of temporary movement into and out of the study area (represented by the γ parameters). Therefore, interpreting the biological significance of estimates for apparent survival differs between the Pradel and RD approaches.

In each case, apparent survival differs from true survival in that apparent survival is confounded with emigration out of the study area. The notion of emigration can further be decomposed to describe either temporary emigration (i.e., an individual becomes temporarily unavailable for capture) or permanent emigration (i.e., an individual becomes permanently unavailable for capture or permanently leaves the system). Because trap nets in this study were set in the near-shore area of the lake, individuals that stayed in the middle of the lake would be considered unavailable for capture. Any fish that permanently left the system, presumably via the

outlet of the lake, would be considered to have permanently emigrated. Permanent emigration is confounded with survival in both the Pradel models and the RD models, contrasting with temporary emigration that is confounded with survival only in the Pradel models.

The γ parameters of the RD, which refer to movement in and out of the study area, are also interpreted as the probability of being available for capture. In other words, if an individual is in the study area and therefore available for capture, that individual has a non-zero chance of being detected or captured. Since the γ'' parameter refers to the probability of an individual staying available (available at time *i* given that it was also available at time *i* - 1), 1 - γ'' is interpreted as the probability that an individual becomes unavailable for capture at time *i* (i.e., it temporarily emigrates) given that it was in the study area at time i.

The preliminary step of the RD analysis, in which I assessed the identifiability of the γ parameters, produced some unexpected results. The "no movement" models (Kendall et al. 1997) in which γ'' and γ' were fixed to one and zero, respectively, received the highest AIC_c weights for both lakes, suggesting that individuals tended to stay in their respective states in these lakes throughout the study period. Furthermore, the parameter estimates for γ'' and γ' in the less supported Markovian and random movement models, when estimable, tended to be close to the bounds of one and zero, respectively, explaining the difficulties in numerical convergence of these estimates and providing more evidence that the "no movement" models best fit the data. There are two likely biological interpretations for these results. First, any brook trout that live in the pelagic zone, or in the deepest part of the lakes, stay exclusively in those areas in the early spring when the sampling was conducted. The second interpretation is that all individuals in each lake were at risk of being captured in the spring trap net occasions and that the unavailable state did not exist or was too small in size to allow a significant number of fish to escape detection.

The first conclusion seems unlikely. Mucha and Mackereth (2008) found that brook trout in Nipigon Bay, Lake Superior were found almost exclusively in the shallow nearshore areas in the early spring before moving deeper in the summer months. These fish also exhibited strong diurnal migration patterns, moving to extremely shallow depths during the night. Another study by Bourke (1997) found that individual brook trout tended to prefer either a pelagic or benthic habitat in two small Canadian lakes. That author noted, however, that the pelagic group – which represented only 18% of all the individuals – showed less site fidelity than the benthic group, often traveling greater distances at night. The pelagic fish were detected in the littoral/benthic zone approximately 30% of the time (Bourke 1997). Both of these studies suggest that all brook trout may encounter sampling gear deployed in the littoral zones in lakes.

Under the "no movement" γ parameterization, the estimates of apparent survival represent the probability that an individual dies or permanently emigrates. Permanent emigration of lentic brook trout has been found to be primarily associated with spawning behavior and is unlikely to occur in the spring. Furthermore, an emigration study conducted on both East Lake and Panther Lake in the fall of 2007 and 2008, estimated less than 5% emigration by brook trout from both lakes (AFRP unpublished data). In the case that permanent emigration is determined to be negligible or nonexistent, *S* would represent the true survival of the available population. Due to the likely absence of an unavailable state in this study, the *S* estimates represent true survival for the entire population and the *N* estimates represent the total number of fish in the system.

Closure

Boulanger et al. (2002) proposed testing for closure by fitting a model set using the Pradel survival and recruitment parametrization that estimates apparent survival (φ), recruitment (f), and capture probability (p) (Pradel 1996). The recruitment parameter (f) represents the number of individuals added to the population, while the apparent survival (φ) represents the total number of individuals no longer present in the population. As previously mentioned, temporary and permanent emigration seem unlikely over the sampling period in this study. Therefore, the φ parameter likely represents subtractions from the populations due to mortality during each primary sampling occasion. Similarly, if all fish were available for capture, no emigration could occur from an unavailable state, and f strictly represents the additions due to recruitment. Recruitment, as defined in this study, differs from recruitment in the traditional sense. Only fish greater than 150mm were tagged during the sampling occasions, therefore "recruitment" refers to fish that grew large enough to become available for tagging. If no unavailable state exists, then the likelihood of temporary immigration would be zero, and f would represent the number of fish that grew large enough to be tagged, given that they were too small to be tagged at the beginning of the study. Since growth is minimal over such a small time-scale, the notion that closure was violated due to recruitment is extremely unlikely.

Interestingly, the results from the Pradel models provide some evidence that the population was not closed during the sampling events in 2010 and 2013 in East Lake due to φ being estimated as less than one. In other words, there was a non-zero chance of an individual leaving the study system. Since the probability of emigration is at or near zero, the resulting violation in closure can safely be attributed to mortality. It is possible that brook trout experienced mortality over the course of the sampling period. In a study by Hutchings et al.

(1999), water content in brook trout body tissue increased, while lipid content simultaneously decreased, over the course of the winter months. This results in a continuously decreasing probability of survival until an individual begins to actively feed again in the spring (Hutchings et al. 1999). Since the trap nets were set immediately following ice out, any fish caught in these nets would be collected at a time when brook trout are most vulnerable to overwinter mortality. In addition, it is also possible that some individuals died from handling. Any fish that were considered dead or dying at the time of capture were not given a tag, but if a marked individual was recaptured dead, the tag was recorded and the individual was never detected alive again. Though handling mortality was low throughout the study (seven tagged fish in East Lake and twelve tagged fish in Panther Lake were either dead in the net or died during handling), each tagged individual that was removed due to sampling (from any capture effort conducted throughout the year) would result in an artificial decrease in the estimates for S and p, which would bias the N estimate high. The S and p estimates would also be biased low by a violation of closure due to mortality during the course of the primary sampling occasion, also resulting in an artificially inflated N estimate for that year. Additionally, this type of closure violation would increase the support for models that account for trap shyness under the closed capture abundance and RD parameterizations.

Advantages of the RD

The RD approach has distinct advantages over CJS models for estimating survival, primarily because the estimates of apparent survival tend to be more precise in the RD framework. As its name suggests, this approach enables robust parameter estimates despite unequal detection probabilities within each primary occasion (Pollock 1982). Catch rates

declined throughout each primary occasion during most years of this study, and this was reflected in the estimates for detection probabilities. This trend would not be detected under the CJS approach, as each primary occasion corresponds to a single estimate for detection probability. The CJS model structure is analogous to the time-invariant detection probability models in the RD that received very little support in the preliminary analysis. Additionally, the RD parameterization allows for the direct estimation of the probability of transitioning between available and unavailable states, whereas the CJS does not. Overall, I found strong evidence to suggest that brook trout in both study lakes did not leave the study area. Under this scenario the reduction in catch rates would be attributed to reductions in encounter probability and not to temporary emigration. This distinction could not be made using the CJS models because γ'' and γ' are not included in the parameterization. As a result, temporary emigration is confounded with detection probability under the CJS framework (Barker 1997, Kendall et al. 2013).

The advantage of the RD approach versus the (within-year) closed capture abundance approach stems from the addition of multiple years of CMR data. The individual closed capture abundance models yielded less precise abundance estimates compared to the estimates resulting from the RD analysis. This is an expected result, as the additional years of data refine the *p* and *c* estimates across multiple years. Additionally, individuals that were not detected at least once for a given year are not included in the data set for the closed capture within-year abundance estimates. As a result, the sample size is consistently smaller for the within year data sets, which results in larger variances surrounding the abundance estimates.

Disadvantages of the RD

The addition of parameters associated with movement and detection probabilities increase the demand for data when using the RD approach. This represents a major drawback of the RD versus simpler model types. The inestimability of several parameters in this study was likely caused by sparse data. Data cloning and simulated annealing often failed to aid the numerical convergence of estimates for detection probabilities in the most general models. This suggests that the data were too sparse to fully partition initial detection probability (p) from subsequent detection probability (c). As a result, I was not able to fully explore the impact of trap effects in the sampling process. Instead, the p = c models were used to test the main-effects model set. While this constraint may have yielded less precise estimates of the other parameters in the RD models than more general models, the p = c models still enable more precise estimates than the CJS models.

The estimated decline in the population of brook trout in Panther Lake presented another challenge in terms of the predictive power of the available data. The number of unique individuals caught decreased from 638 in 2012 to 98 in 2013. The smaller sample sizes led to an increase in uncertainty around the parameters in later study years for Panther Lake, and the power of the data to determine the fit of each model was diminished. The resulting uncertainty in the model selection process obscured the relative importance of each model, as well as the relative ability of environmental covariates to predict changes in survival. Researchers applying CMR techniques to evaluate large-scale mortality events should be mindful of the impact that a reduced sample size will have on the parameter estimation process.

Additional gill net, trap net, and angler catch data, which were available for each of these lakes, might have been incorporated into a more complex analysis that would allow for

encounters outside of the primary sampling time-frame. However, adding these data incorporate a tradeoff because more complex model types (e.g., Barker RD models) (Barker 1997, Kendall et al. 2013) involve more parameters that, in turn, increases the demand for data. For this study the additional data were too sparse to justify the use of the Barker RD, as many of the additional parameters for this model type were extrinsically nonidentifiable.

Despite the limitations of these available data, the RD approach allowed for a robust estimation of abundance and survival, while enabling the evaluation of the relative importance of temperature metrics as predictors of survival. Unfortunately, I was unable to take full advantage of the potential of this particular model type due to low recapture rates. I strongly recommend that future iterations of this sampling design involve efforts to increase detection rates. This can be achieved in several ways. Adding additional secondary occasions increases the likelihood that an individual will be detected at least once (p^*) during each primary occasion. Incorporating the use of passive integrated transponder (PIT) tags and readers into the sampling scheme may prove useful in encountering individuals who encounter the gear and fail to be captured, increasing the number of recaptured individuals. Individuals not detected in the final year in a study may be encountered again if additional primary sampling occasions are conducted. Adding additional years to a RD study would be particularly useful for longer-lived organisms and in systems that contain a substantial unobservable area (Williams 2002). Although extending the number of primary occasions would undoubtedly increase the cost of a given study, researchers should weigh the potential benefits of increasing precision of the S and γ parameters against the additional costs, particularly if these are the parameters of greatest interest.

Implications

Few researchers have been able to make a direct connection between wild brook trout survival and thermally stressful conditions using CMR techniques. Using a CMR approach similar to the one used in this study, Letcher et al. (2015) found that brook trout survival was correlated with water temperature in several stream networks. However, maximum summer water temperature in that study never approached thermally stressful levels, and the observed correlation resulted primarily from the interaction effect between temperature and growth on survival (Letcher et al. 2015). To my knowledge, the RD study described in this thesis represents the only *in situ* study in which environmental temperature covariates were used to model apparent survival in a wild brook trout population exposed to thermally stressful conditions. Furthermore, the inclusion of a stratified lake in this study provided a unique comparison of the relative influence of elevated summer water temperatures on survival of two wild, lentic brook trout populations living under contrasting thermal regimes.

These findings provide evidence that chronic thermal stress has a greater impact than acute stress on reduced survival in a lentic brook population. While this study focused exclusively on brook trout, similar effects have been measured in other salmonine fishes (Biro et al. 2007). It is also important to note that my study results suggest that predicting future abundance of these cold-water fish based solely on maximum temperatures may lead to misleading results. Predictive modeling approaches that fail to account for the duration and magnitude of thermal stress events will likely be unsuccessful in predicting range declines and risk of local extirpation of salmonine fishes. Furthermore, since the presence of cold water refugia mitigate these effects, failure to account for the presence of thermal refugia will overestimate the impacts of thermal stress as the earth's climate continues to warm.

Brook trout and other cold-water species face an uncertain future in the face of climate change. Assessing the potential influence of temperature on salmonine fish populations can be challenging, therefore it is critical to incorporate techniques that best describe this relationship. As the climate warms, researchers will likely have increased opportunity to study range declines and extirpations (McCullough et al. 2009) of these species. Therefore, it will be increasingly important to implement cost-effective methods to study cold-water fish population parameters while maximizing precision of the resulting survival and abundance estimates. The results from the analyses described in this study should prove useful to future conservation efforts as a means to demonstrate how to characterize population level responses to climate change.

APPENDIX A

ABUNDANCE OF BROOK TROUT IN WILMURT LAKE

Introduction

The quality of a thermal refuge can be compromised by a depletion of dissolved oxygen which often occurs during the late summer months (Jankowski et al. 2006). This situation often results in a phenomenon referred to as a "thermal squeeze" in which thermally optimal hypolimnetic waters become sub-optimal due to dissolved oxygen limitation (Nestler et al. 2002). Wilmurt Lake is an example of a system that stratifies in the summer, but only offers a limited oxygen-rich thermal refuge. In order to assess the impact this might have on the abundance of a lentic brook trout population, a third CMR recapture study was conducted in Wilmurt Lake from 2012 to 2014.

Methods

Wilmurt Lake is considerably larger than both East Lake and Panther Lake, with a surface area of 38.8 hectares and a maximum depth of 10.7 meters. Wilmurt Lake is located entirely on private property in Hamilton County, NY. Brook trout are the only fish species present in Wilmurt Lake.

The Wilmurt Lake component of the CMR study was conducted from the spring of 2012 through the spring of 2014. To characterize the extent and quality of the hypolimnion, full temperature and dissolved oxygen profiles were conducted in Wilmurt Lake at 0.5 m intervals in mid-July and mid-August using a YSI® probe for each of the three years in the study (Figure A.1). Field surveys to capture fish in trap nets were conducted in a similar fashion to the methods

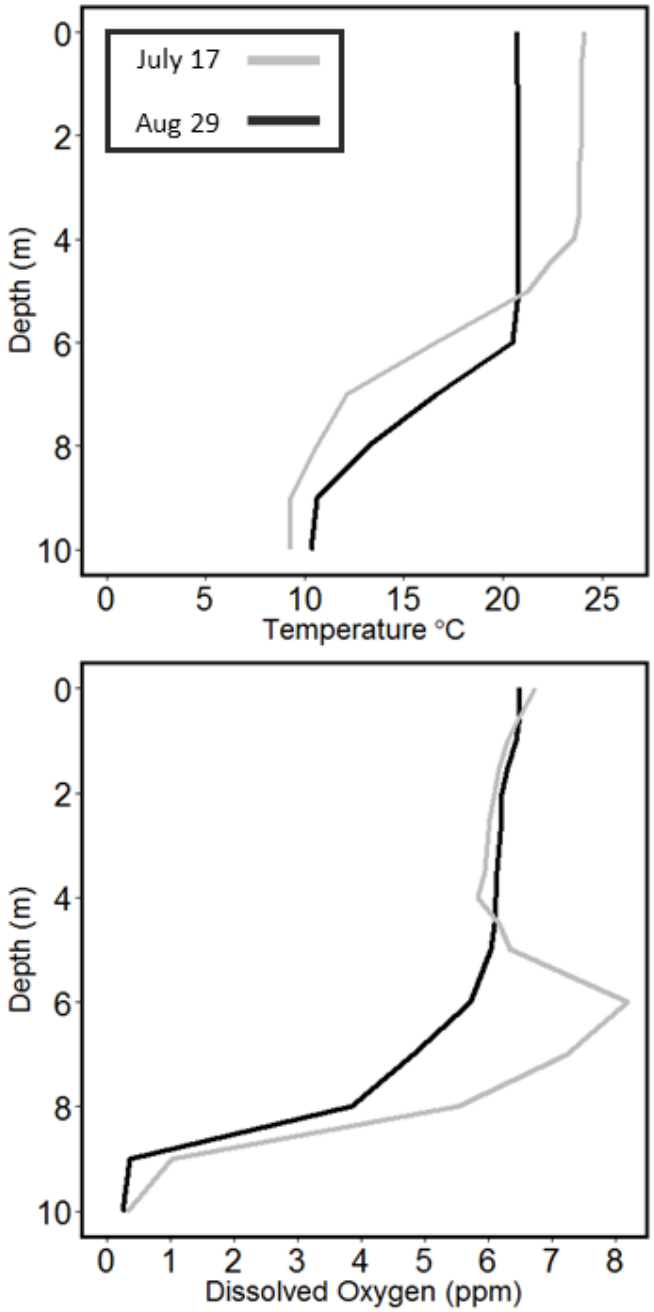

Figure A.1. Temperature and dissolved oxygen profiles from Wilmurt Lake from the summer of 2012.

described in Chapter 1 (Table A.1, Figure A.2). The same candidate model sets used in Chapter 1 were included for the closure tests (using Pradel models) (see Chapter 1). The within-year closed capture abundance estimates yielded identifiable parameters for models in which p was not equal to c, and these models were included in the RD analysis. Individual covariates of *LENGTH* (see Appendix B), were incorporated in each analysis. Due to the limited number of primary occasions, the preliminary modeling of the γ parameters in the RD analysis did not include the Markovian movement models (Kendall et al. 1997), as they were structurally equivalent to the time invariant models. As was the case with East and Panther lakes, the "no movement" models proved to be the most parsimonious models for which all parameters were estimable and were used exclusively in the RD analysis for Wilmurt Lake. The candidate model set consisted of both time-varying and constant survival models combined with each of the four standard (Otis et al. 1978) models, with and without *LENGTH* as a covariate (Table S.6). The model set was fit to the data in program MARK 8.0 (White and Burnham 1999). Simulated annealing was employed in cases where parameter estimates failed to converge, and any models which yielded unidentifiable parameters were removed from the analysis. The remaining models were ranked using Akaike's information criterion (AIC; Akaike 1973) adjusted for small sample size (AIC_c; Hurvich and Tsai 1989). Model averaged estimates of *S* and *N* were obtained by multiplying the Akaike weights (i.e., the likelihood that a given model most parsimoniously describes the data) by the parameter estimates given by each model (Burnham and Anderson, 2002).

Table A.1. Initial captures and recaptures from Wilmurt Lake for spring trap net samples (all secondary occasions combined). The number of newly tagged fish plus individuals recaptured at least once (i.e., # of unique tags recorded) is represented by M_{t+1}.

Year	Tags Applied	Recaptures	Total	M_{t+1}
2012	245	31	276	250
2013	202	45	247	227
2014	182	23	205	192

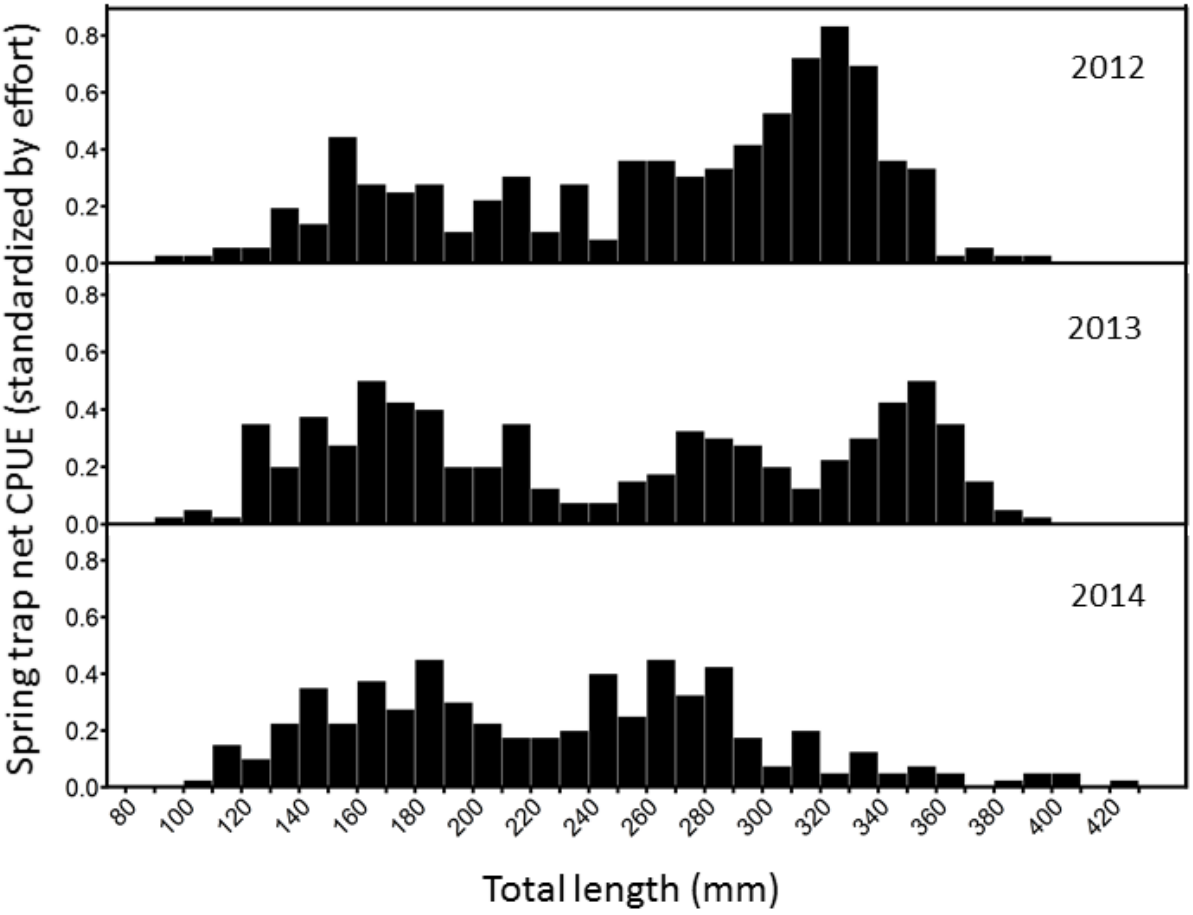

Figure A.2. Length frequency histogram of the spring trap net catch from 2010 to 2014 in Wilmurt Lake, standardized by effort.

Results and discussion

The results from the RD analysis suggest that the population of brook trout >150 mm in Wilmurt Lake remained relatively stable throughout the three years of the study (Figure A.3). The population did not show a significant decline between the spring of 2012 and the spring of 2013 (Figure A.4). This stability in the population suggests that a substantial mortality event did not occur during the hot summer of 2012, though the data could not provide the precision needed to detect slight changes in abundance. These estimates contrast with the substantial observed decline in brook trout abundance in Panther Lake over the same time period and provide some evidence that the presence of a thermal refuge in Wilmurt Lake was sufficient in preventing large-scale mortality due to thermal stress.

The within-year closed capture models show strong support for trap effects (Table A.2). Many of the parameters were not identifiable under the Pradel parameterization, most likely due to sparse data. The results from the Pradel models suggest that the assumption of closure was not significantly violated in any year, as indicated by the lack of support of alternative models for which the φ and f parameters were identifiable. Interestingly, weak support for a violation of closure, due to recruitment, was represented by the cumulative AIC_c weights in the model set for 2014 (Table A.3). While not substantial enough to be considered significant, this finding suggests the possibility that some individuals may have entered the population during the spring 2014 trap net occasions. As discussed in Chapter 1, violations of closure due to recruitment are most likely due to immigration rather than from recruitment into the >150 mm size class. This suggests that an unavailable state may exist in Wilmurt Lake, from which individuals may have entered the study area over the course the 2014 sampling time frame.

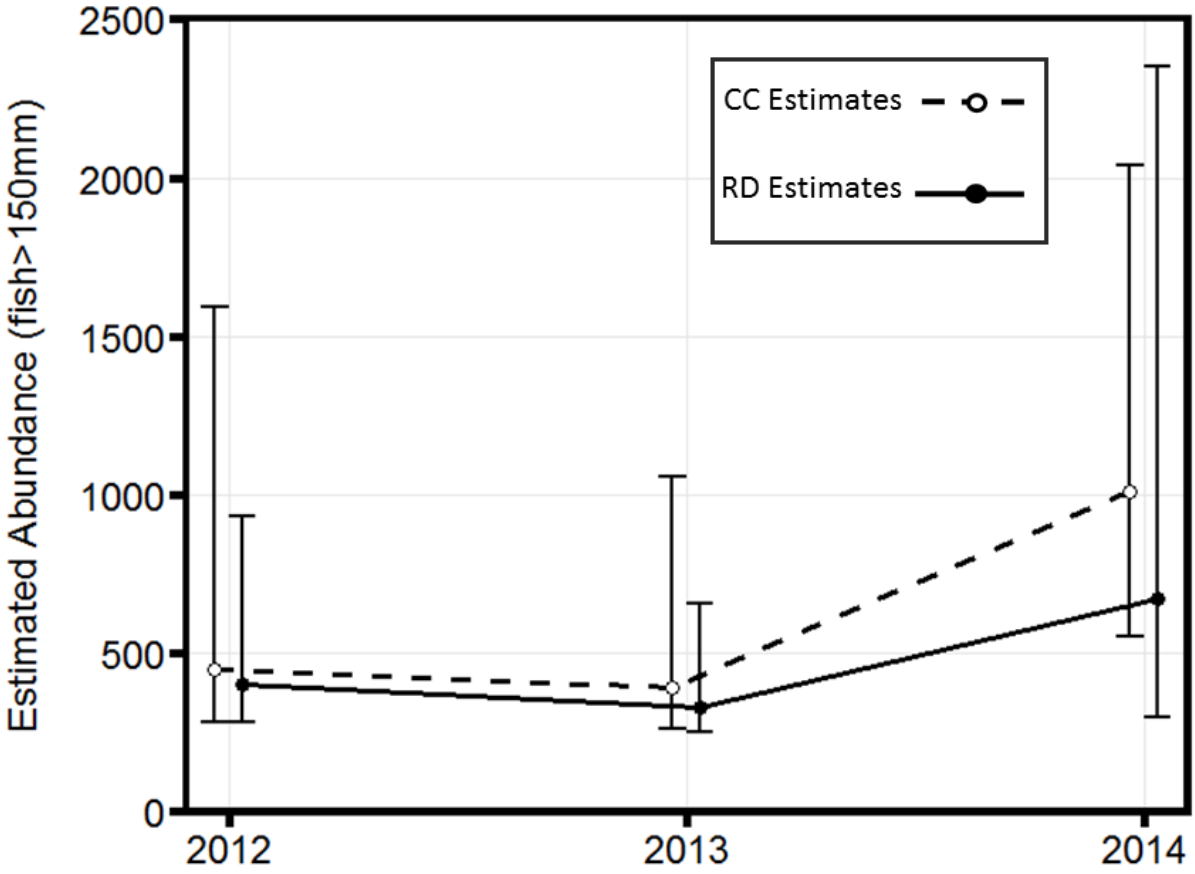

Figure A.3. Within-year closed capture abundance estimates and those obtained from the RD approach for Wilmurt Lake from 2012 to 2014.

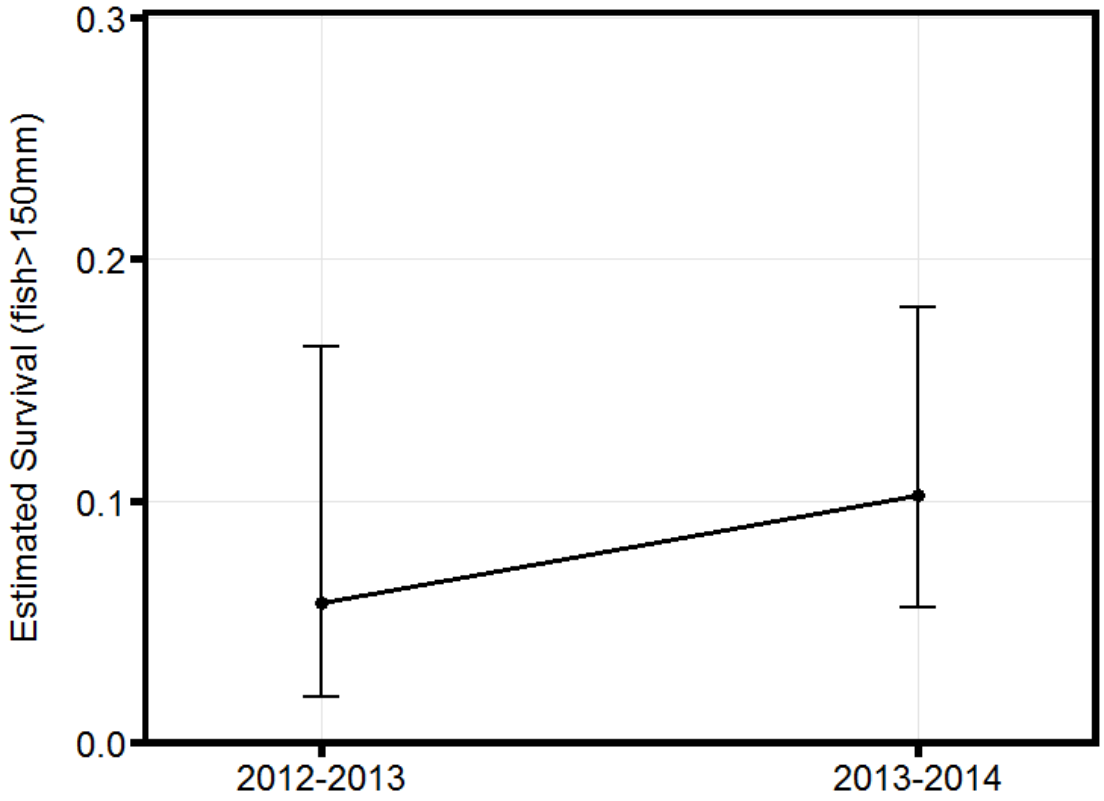

Figure A.4. Estimated annual survival of the available population of brook trout >150 mm in Wilmurt Lake (RD approach).

Table A.2. Model selection results from the within-year closed capture models for Wilmurt Lake.

	Model	ΔAIC_c	AIC_c weight	*K*	Likelihood
2012	*p(.(LENGTH+LENGTH^2)) c(.(LENGTH+LENGTH^2))*	0.00	0.786	6	1.000
	p(t(LENGTH+LENGTH^2)) c(t(LENGTH+LENGTH^2))	3.36	0.146	9	0.186
	p(.(LENGTH)) c(.(LENGTH))	6.76	0.027	4	0.034
	p(.) c(.)	7.69	0.017	2	0.021
	p=c(t(LENGTH+LENGTH^2))	8.68	0.010	5	0.013
2013	*p(.(LENGTH+LENGTH^2)) c(.(LENGTH+LENGTH^2))*	0.00	0.822	6	1.000
	p(t(LENGTH+LENGTH^2)) c(t(LENGTH+LENGTH^2))	3.74	0.127	9	0.155
	p(.(LENGTH)) c(.(LENGTH)	5.94	0.042	4	0.051
2014	*p=c(t)*	0.00	0.459	3	1.000
	p(t) c(t) [p_i=c_i]	1.45	0.222	4	0.484
	p=c(t(LENGTH))	2.03	0.167	4	0.363
	p=c(t(LENGTH+LENGTH^2))	3.88	0.066	5	0.144
	p(.) c(.)	4.14	0.058	2	0.126
	p(.(LENGTH)) c(.(LENGTH))	7.66	0.010	4	0.022

Table A.3. Top models from the preliminary modeling of the γ parameters for Wilmurt Lake

Model	ΔAIC_c	AIC_c weight	*K*	Likelihood
S(.) γ''(LENGTH) γ'(FIX1) p=c(.)	0.00	0.270	12	1.000
S(.) γ(No Movement) p=c(.)	0.87	0.175	10	0.649
S(t) γ''(LENGTH) γ'(FIX1) p=c(.)	1.03	0.161	13	0.598
S(t) γ(No Movement) p=c(.)	1.56	0.124	11	0.458
S(.) γ''(LENGTH) γ'(FIX1) p=c(LENGTH)	2.01	0.099	13	0.366
S(.) γ(No Movement) p=c(LENGTH)	2.07	0.096	11	0.354
S(t) γ(No Movement) p=c(LENGTH)	2.56	0.075	12	0.278

The findings from the γ modeling further support the idea that an unavailable state may exist in Wilmurt Lake (Table A.4). Several models converged on estimates of γ'' when γ'' was held constant over the two years for which it was estimated. The values for γ' were likely inestimable due to their proximity to the boundary of the likelihood surface. When simulated annealing failed to aid convergence, the γ' parameter was fixed to one, and these models were included in the final model set. Model averaging over this model set suggested that the value for γ'' may deviate from zero. The biological interpretation of this finding is that (i) an unavailable state may exist in Wilmurt Lake, and (ii) that individuals available for capture in a given year may temporarily emigrate to an area of the lake that makes them unavailable for capture in subsequent sampling occasions. This *a posteriori* approach is likely subject to error and I do not recommend inference based on this result. Instead, this finding may motivate future studies designed to ascertain if, in fact, such an unavailable state exists. Regardless, the "no movement" models were the only *a priori* models for which the γ estimates converged. As a result, the subsequent RD analysis exclusively contained the "no movement" parameterization (Table A.5).

The findings from the Wilmurt Lake analysis contribute circumstantial evidence that a hypolimnetic thermal refuge that is restricted in extent due to oxygen depletion may prevent substantial mortality during exceptionally hot summers. More importantly, these findings serve as an example of how sparse data can limit robust inference of the influence of environmental factors on survival and abundance using complex CMR analyses. Such inference would be substantially improved by incorporating data obtained from the addition of both secondary and primary sampling occasions. Despite its limitations, the Wilmurt Lake study produced some informative results that could provide the basis for future study of this fish population and aid in the refinement of the design of future surveys in this lake.

Table A.4. Model selection results from the Pradel models with recruitment for Wilmurt Lake. *K* = number of parameters. Each model includes Survival (φ), detection probability (p), and recruitment (*f*) parameters. For each parameter, "*T*" represents a trend, "*t*" represents time variation, "." indicates that the parameter was held constant, and "*FIX*" indicates that the parameter was fixed. Closure is represented by fixing survival to 1 and fidelity to 0.

	Model	ΔAIC_c	AIC_c weights	*K*	Likelihood
2012	*φ(FIX 1) p(T) f(FIX 0)*	0.00	0.392	2	1.000
	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	1.12	0.224	6	0.572
	φ(FIX 1) p(t) f(FIX 0)	1.67	0.171	3	0.435
	φ(FIX 1) p(LENGTH+t) f(FIX 0)	2.94	0.090	4	0.230
	φ(.) p(.) f(FIX 0)	3.37	0.073	2	0.186
	φ(.) p(.(LENGTH)) f(FIX 0)	4.14	0.050	3	0.126
2013	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	0.00	1.000	6	1.000
	φ(FIX 1) p(t) f(FIX 0)	21.61	0.000	3	0.000
	φ(.) p(LENGTH+t) f(.)	21.92	0.000	6	0.000
	φ(.) p(LENGTH+t) f(FIX 0)	22.05	0.000	5	0.000
	φ(FIX 1) p(LENGTH+t) f(FIX 0)	23.47	0.000	4	0.000
2014	*φ(FIX 1) p(t) f(FIX 0)*	0.00	0.369	3	1.000
	φ(FIX 1) p(t) f(.)	1.50	0.174	4	0.472
	φ(FIX 1) p(LENGTH+t) f(FIX 0)	2.08	0.130	4	0.354
	φ(.) p(t) f(.) .	3.51	0.064	5	0.173
	φ(FIX 1) p(LENGTH+t) f(.)	3.59	0.061	5	0.166
	φ(FIX 1) p(T) f(.)	3.66	0.059	2	0.160
	φ(.) p(.) f(FIX 0)	3.84	0.054	2	0.147
	φ(.) p(.) f(.)	5.70	0.021	3	0.058
	*φ(FIX 1) p(LENGTH*t) f(FIX 0)*	5.85	0.020	6	0.054
	φ(.) p(.(LENGTH)) f(FIX 0)	5.89	0.019	3	0.053

Table A.5. Top models from the main effects RD model set for Wilmurt Lake for AICc weights >0.010. The γ parameters were held constant and are not shown.

Model	ΔAIC_c	AIC_c weight	*K*	Likelihood
S(LENGTH+L^2) p(t(LENGTH+L^2) c(.(LENGTH+L^2))	0.00	0.265	17	1.000
S(LENGTH+L^2) p(.(LENGTH+L^2) c(.(LENGTH+L^2))	0.24	0.235	11	0.887
S(LENGTH+L^2) p(t(LENGTH+L^2)) c(.)	1.69	0.114	15	0.430
S(LENGTH+L^2) p(.(LENGTH+L^2) c(.)	2.00	0.098	9	0.368
S(.) p(t(LENGTH+L^2) c(.(LENGTH+L^2))	2.46	0.077	15	0.292
S(.) p(.(LENGTH+L^2) c(.(LENGTH+L^2))	3.38	0.049	9	0.185
S(t) p(.(LENGTH+L^2)) c(.(LENGTH+L^2))	3.92	0.037	10	0.141
S(.) p(t(LENGTH+L^2)) c(.)	4.18	0.033	13	0.124
S(t) p(t(LENGTH+L^2)) c(.(LENGTH+L^2))	4.48	0.028	16	0.107
S(.) p(.(LENGTH+L^2)) c(.)	5.16	0.020	7	0.076
S(t) p(.(LENGTH+L^2)) c(.)	5.69	0.015	8	0.058
S(t) p(t(LENGTH+L^2)) c(.)	6.18	0.012	14	0.046

APPENDIX B

LENGTH AS AN INDIVIDUAL COVARIATE FOR USE IN ROBUST DESIGN MODELS

Introduction

Incorporation of continuous time-varying individual covariates into capture-mark-recapture (CMR) models can lead to substantial increases in the precision of parameter estimates (Pollock 2002). These types of covariates (length, mass, etc.) are commonly collected during sampling and are often available to researchers as a result, but these measurements are not available for individuals that were not encountered during the sampling process. Therefore, incorporating time-varying individual covariates into the modeling approach can be challenging, as a large proportion of these values may be missing from the data. Several methods for dealing with missing covariates have been proposed (Bonner et al. 2010), and this topic is currently a subject of active research and debate (Schofield and Barker 2011).

The most commonly used approaches could be placed into one of two categories. In the first approach, Bayesian modeling techniques allow for parameter estimation based on the available data; the relative influence of an individual covariate on parameter estimates is only evaluated for occasions in which an individual was detected and the covariate collected. The second approach involves imputing the missing covariate values based on some generating model, such as a logistic growth equation. The advantages and disadvantages of each approach are discussed at length by (Bonner et al. 2010) in which each technique was applied to data from a well-documented population of Soay sheep on the Isle of Hirta, Scotland. Each approach was shown to be effective in modeling the influence of continuous time-varying covariates on detection and survival when modeling of the covariate accurately approximated the true data-

generating mechanism (Bonner et al., 2010). I used the second approach to computationally impute missing length covariate values for the robust design (RD) analysis described in chapter 1 of this thesis. Individual length was directly measured (not estimated) for the other analyses from chapter 1.

Methods

A von Bertalanffy growth curve (von Bertalanffy 1938) was fit to age at length data obtained from brook trout collected from 2005 to 2013 using the "fishmethods" package in R v.3.2.4 (Nelson 2014). The total length of each fish was measured to the nearest millimeter, and a separate length at age relationship was derived for each study lake. To develop this relationship, a sagittal otolith ('otolith' hereafter) taken from each fish was cleaned, dried and processed before age at final capture was determined by two independent readers (Koenigs et al. 2015). Age estimates from both readers were made without knowledge of fish length or mass, and only age estimates agreed upon by both readers were used in the subsequent analysis.

Estimating length

I first estimated age in days at first capture for every fish using the results from the von Bertalanffy curve. Length at each subsequent primary sampling occasion was then estimated by first calculating the increase of age in days between sampling occasions, and then estimating length using the growth constant from the von Bertalanffy model. In cases where an individual was encountered multiple times, the estimated age in days at first capture was adjusted to minimize the difference between observed length and estimated length. Maximum estimated length was set equal to the maximum length observed for brook trout in each lake during the RD

sampling period. Because these covariates were being imputed for use in analysis by program MARK, estimating length prior to first capture was not necessary, as program MARK ignores such individual covariate values.

Results and Discussion

A total of 275 fish from East Lake, 262 fish from Panther Lake, and 213 fish from Wilmurt Lake were aged using otoliths. Results from the otolith aging indicate that the fish in East Lake lived longer than the fish in Panther and Wilmurt lakes. The oldest fish from East Lake were estimated to be ten years old (N=2), while the oldest fish in Panther and Wilmurt lakes were estimated to be only five years old (N=3, N=5, respectively). Growth constants obtained from the von Bertalanffy curve indicate that growth rates were reduced in East Lake by comparison with the other two lakes (Table A.6, Figure A.5).

The fit of the growth curve is likely to be influenced by the lack of data points at the larger lengths. Any data points at extreme maximum lengths have substantial leverage and influence on the curve due to the reduced number of samples. Therefore, any variability in the length-age relationship for fish approaching the maximum length would be poorly accounted for in the model, and the model fit at this extreme might not be appropriate. The lack of data from larger fish resulted from a sampling bias toward smaller fish in lakes where anglers are interested in catching large fish. The uncertainty involved with the estimated lengths of larger fish underpinned the motivation for setting the maximum estimated length equal to the maximum observed length of fish from each lake.

Table A.6. Length at t_∞ and growth constants (K) for the von Bertalanffy growth curves.

Lake	Length at t_∞	K
East Lake	375.2	0.251
Panther Lake	428.7	0.483
Wilmurt Lake	404.7	0.411

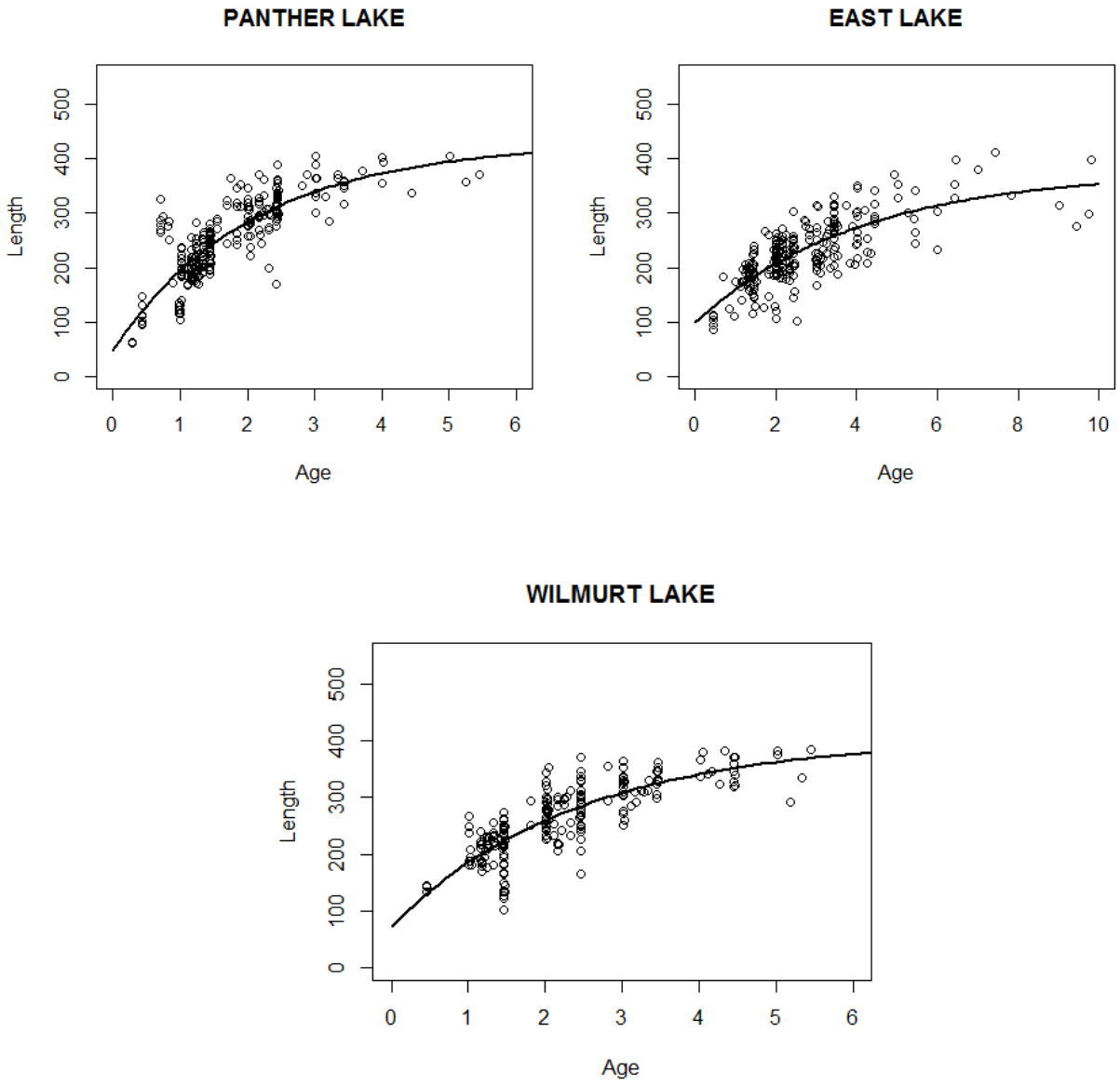

Figure A.5. Plots of the von Bertalanffy growth curves fit to length at age data for brook trout in Panther Lake, East Lake and Wilmurt Lake.

APPENDIX C

CATCH CURVE, BEVERTON-HOLT, AND CHAPMAN-ROBSON ESTIMATES OF ANNUAL MORTALITY

Introduction

Catch curve analyses provide rough estimates of annual survival based on the age-frequency data from fish sampled in a single year (cross-sectional data) or from following a cohort of fish over time (longitudinal data) (Ricker 1975, Tuckey et al. 2007). The two most commonly used approaches include a linear regression based approach (Ricker 1975, Seber 1982) and the Chapman-Robson (1960) estimator (CR). Both methods rest on the assumption that mortality remains constant over time for fish that are fully recruited to the sampling gear. Recruitment (i.e., additions to the population susceptible to capture) and vulnerability to the sampling gear are also assumed to be constant for each year in the study and across age groups. Additionally, age determination is assumed to be accurate for each individual. Violations to these assumptions, and the resulting biases, have been evaluated in numerous studies (Dunn et al. 2002, Smith et al. 2012), and most authors recommend the CR estimator for estimating mortality/survival from age-frequency data. The intention of this appendix is to ascertain if the annual survival estimates (S) obtained through the approach in Chapter 1 are somewhat similar to annual survival estimates obtained through more traditional methods. This section is not intended to serve as a formal comparison between the various methods.

Methods

Catch curves and CR estimators were fit to the data collected during the spring trap net samples from the three study lakes (see Chapter 1 and Appendix A methods). Since these fish

were released alive in the mark-recapture study, ages could not be determined by otolith ageing. Instead, age was estimated by using the von Bertalanffy applied to the measured length of each fish (see Appendix B) and rounded to the nearest year class. This method assumes equal variance between year classes. All CR estimators, as well as cross-sectional and longitudinal catch curves, were based on these estimated ages and were calculated using the "FSA" package v.0.8.11 (Ogle 2016) in R v.3.3.2. Estimates of instantaneous mortality (*Z*) were also calculated using the Beverton-Holt estimator, with and without the Ehrhardt and Ault (1992) bias-correction (see Quinn and Deriso 1999) based on the original length data, using the "fishmethods" package in R (Nelson 2014).

Results and Discussion

Overall, the results from these analyses were highly inconsistent between years and across methods (Table A.7, Table A.8). For example, the S estimates in Panther Lake ranged from 0.16 (catch curve) to 0.45 (uncorrected Beverton-Holt estimator) based on the data collected in 2011. The corrected Beverton-Holt estimator produces annual survival estimates for fish in Panther Lake that ranged from 0.16 to 0.51. East Lake was estimated to have better survival, overall, than Panther Lake. However, caution is advised when interpreting these results. Most important, these estimators rely on the assumption that survival (and other population parameters) remain constant between years, therefore annual variation in S would, be a violation of that underlying assumption; perceived trends or conspicuous deviations in S should not be interpreted as a change in *S* from one year to the next. Instead, the inconsistencies among the estimators within a year – and between years – could result from changes in: survival, recruitment, detection probability, and/or growth. Additionally, each of these estimators depend

on the growth coefficients from the von Bertalanffy model (see the caveats in Appendix B), therefore any error in age estimation would translate into error in the calculation of mortality rates. Furthermore, the sample sizes in many years of this study were insufficient for these analyses to perform as intended. With enough data, and accurate ageing techniques, catch curves and the other estimators may be well suited to provide insight into the dynamics of stable populations. It seems that neither the cross-sectional analysis (Table A.7, Figure A.6), nor the longitudinal analysis (Table A.8, Figure A.7), in this instance, can be relied upon to provide additional support for the findings from Chapter 1.

Table A.7. Estimates of instantaneous mortality (Z) and annual survival (S) for the catch curve (CC), Chapman-Robson (CR), Beverton-Holt (BH), and bias corrected Beverton-Holt (BH_{corr}) estimators based on cross-sectional data. The * represents insufficient data.

	2010				2011				2012				2013				2014			
	Z	SE	*S*	SE	*Z*	SE	*S*	SE	*Z*	SE	*S*	SE	*Z*	SE	*S*	SE	*Z*	SE	*S*	SE
Panther Lake																				
CC	1.362	0.071	0.26		1.837	0.117	0.16		1.236	0.170	0.29		0.825	0.106	0.44		0.730	0.266	0.48	
CR	1.289	0.049	0.26	0.07	1.382	0.039	0.21	0.13	0.955	0.142	0.36	0.11	0.729	0.081	0.45	0.26	0.858	0.215	0.39	0.37
BH	1.565	0.065	0.21	0.06	0.805	0.032	0.45	0.03	0.591	0.023	0.55	0.02	1.211	0.121	0.30	0.11	1.126	0.147	0.32	0.14
BH_{corr}	1.825	0.068	0.16	0.07	0.883	0.039	0.41	0.04	0.669	0.023	0.51	0.02	1.438	0.185	0.24	0.17	1.381	0.176	0.25	0.16
East Lake																				
CC	0.962	0.167	0.38		0.637	0.038	0.53		0.750	0.111	0.47		0.735	0.095	0.48		0.666	0.063	0.51	
CR	0.870	0.096	0.41	0.08	0.650	0.039	0.50	0.12	0.530	0.075	0.57	0.16	0.773	0.077	0.44	0.11	0.513	0.043	0.58	0.12
BH	0.601	0.015	0.45	0.02	0.443	0.021	0.64	0.02	0.424	0.025	0.65	0.02	0.550	0.021	0.58	0.02	0.398	0.015	0.67	0.02
BH_{corr}	0.637	0.016	0.47	0.02	0.481	0.022	0.62	0.02	0.460	0.025	0.63	0.02	0.590	0.023	0.55	0.02	0.434	0.019	0.65	0.02
Wilmurt Lake																				
CC									0.763	0.120	0.47		0.686	0.112	0.50		*	*		
CR									0.427	0.111	0.64	0.11	0.461	0.067	0.61	0.13	0.629	0.058	0.50	0.17
BH									0.430	0.025	0.65	0.02	0.501	0.035	0.61	0.03	0.715	0.048	0.49	0.05
BH_{corr}									0.487	0.028	0.61	0.03	0.595	0.052	0.55	0.05	0.809	0.053	0.45	0.05

Table A.8. Estimates of instantaneous mortality (Z) and annual survival (S) for the catch curve (CC) and Chapman-Robson (CR) estimators for each cohort based on longitudinal data, using estimated age classes. Bold represents SE > *S*. The * represents insufficient data. Data was insufficient to analyze cohorts for all other year classes.

	2008 Cohort				2009 Cohort				2010 Cohort				2011 Cohort			
	Z	SE	*S*	SE	*Z*	SE	*S*	SE	*Z*	SE	*S*	SE	*Z*	SE	*S*	SE
Panther Lake																
CC	0.865	0.301	0.42		1.466	0.257	0.23		2.256	0.386	0.10		2.142	0.087	0.12	
CR	1.009	0.160	0.33	0.15	1.004	0.146	0.35	0.07	2.161	0.154	0.07	**0.10**	1.792	0.067	0.12	**0.13**
East Lake																
CC	1.009	0.198	0.36		0.667	0.091	0.51		*	*	*		*	*	*	
CR	1.221	0.155	0.27	0.10	0.717	0.071	0.47	0.09	0.423	0.468	0.64	0.11	*	*	*	*

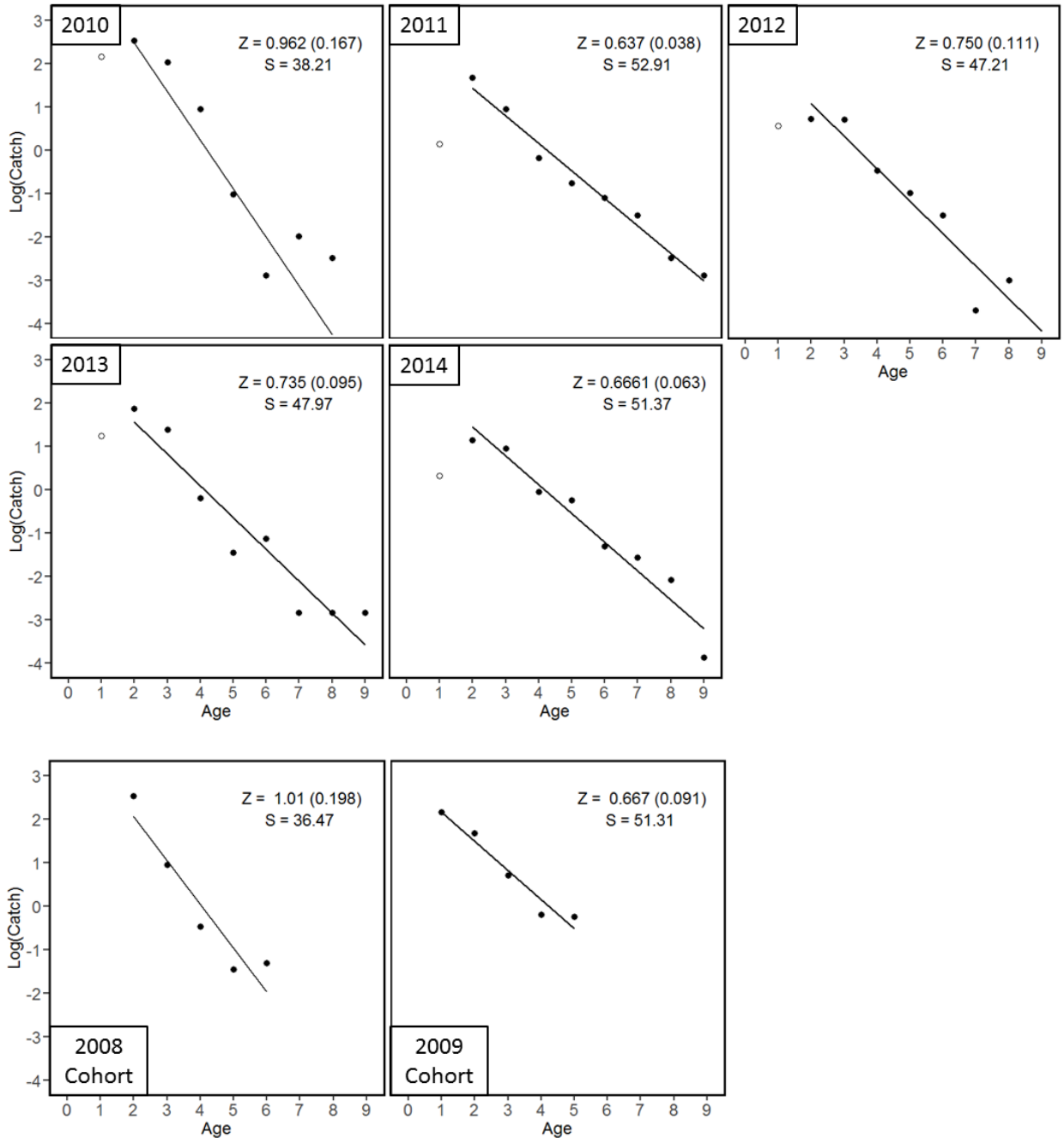

Figure A.6. Cross sectional (above) and longitudinal (below) catch curves for East Lake. Open circles represent ages not included in the regression.

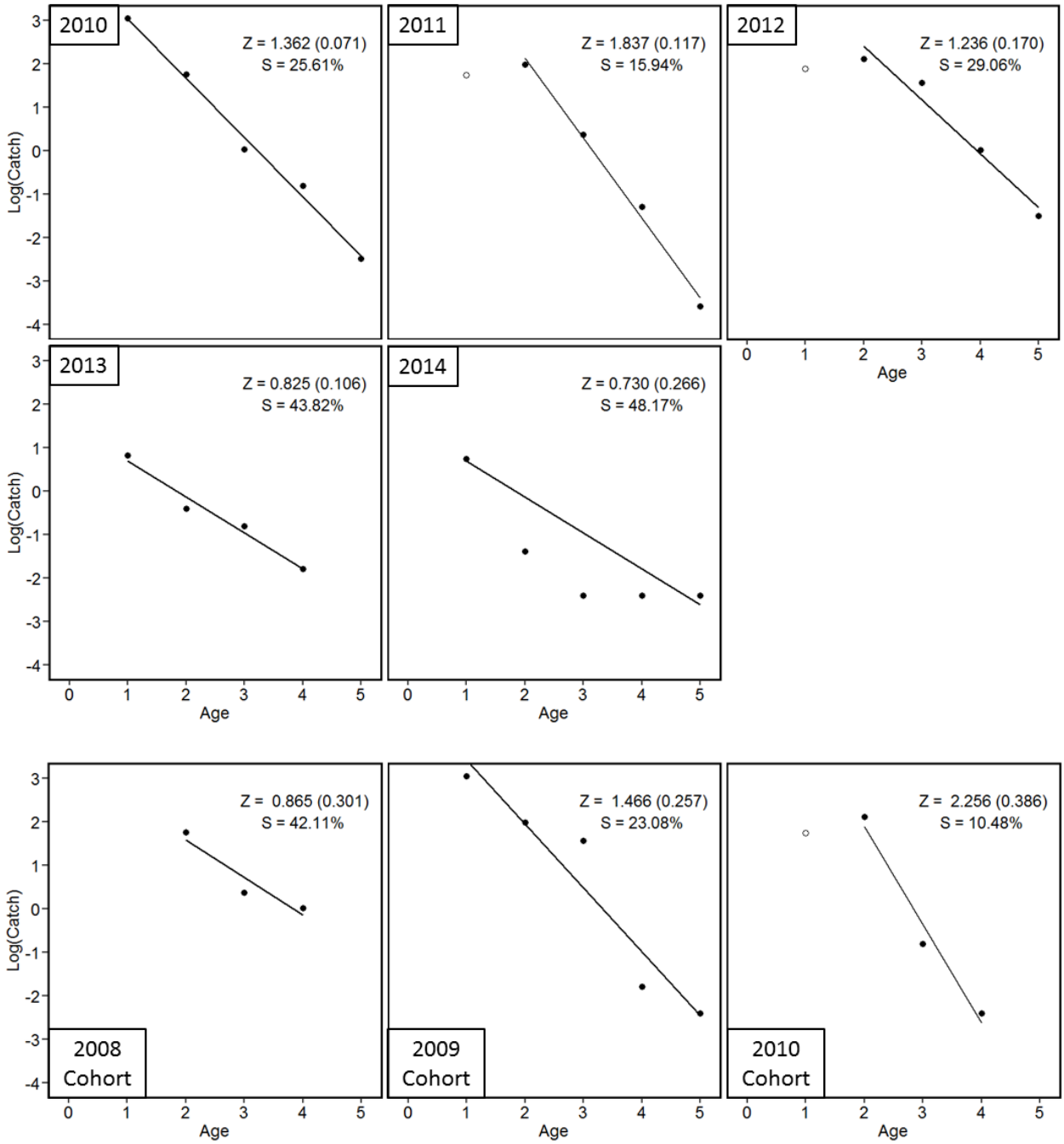

Figure A.7. Cross sectional (above) and longitudinal (below) catch curves for Panther Lake. Open circles represent ages not included in the regression.

APPENDIX D

SUPPORTING INFORMATION

Table S.1. Candidate model set for testing for closure using Pradel models (with recruitment). Models include Survival (φ), detection probability (p), and recruitment (*f*) parameters. For each parameter, "*T*" represents a trend, "*t*" represents time variation, "." indicates that the parameter was held constant, and "*FIX*" indicates that the parameter was fixed.

Model Name
*φ(t) p(LENGTH*t) f(.)*
*φ(t) p(LENGTH*t) f(t)*
*φ(.) p(LENGTH*t) f(t)*
*φ(.) p(LENGTH*t) f(.)*
φ(t) p(LENGTH+t) f(.)
φ(t) p(LENGTH+t) f(t)
*φ(.) p(LENGTH*t) f(FIX 0)*
*φ(FIX 1) p(LENGTH*t) f(.)*
φ(.) p(LENGTH+t) f(.)
φ(.) p(LENGTH+t) f(t)
*φ(FIX 1) p(LENGTH*t) f(FIX 0)*
φ(.) p(LENGTH+t) f(FIX 0)
φ(.) p(.(LENGTH)) f(t)
φ(t) p(.(LENGTH)) f(.)
φ(.) p(.(LENGTH)) f(.)
φ(.) p(.(LENGTH)) f(FIX 0)
φ(.) p(.) f(t)
φ(t) p(.) f(t)
φ(.) p(t) f(.)
φ(FIX 1) p(LENGTH+t) f(FIX 0)
φ(FIX 1) p(LENGTH+t) f(.)
φ(.) p(t) f(FIX 0)
φ(FIX 1) p(t) f(.)
φ(t) p(.) f(.)
φ(.) p(T) f(.)
φ(.) p(.) f(.)
φ(FIX 1) p(t) f(FIX 0)
φ(.) p(.) f(FIX 0)
φ(.) p(T) f(FIX 0)
φ(FIX 1) p(T) f(FIX 0)
φ(FIX 1) p(T) f(.)
φ(FIX 1) p(.(LENGTH)) f(FIX 0)
φ(FIX 1) p(.(LENGTH)) f(.)
φ(FIX 1) p(.) f(FIX 0)
φ(FIX 1) p(.) f(.)

Table S.2. Full candidate model set for the preliminary evaluation of the γ parameters in the RD analysis. Models include initial detection probability (p), and subsequent detection probability (c) as parameters. For each parameter, "t" represents time variation and "." indicates that the parameter was held constant. Both time varying and constant models may be modeled as functions of the *LENGTH* covariates. Additive models are represented by a "+" symbol.

Model Name
S(.) γ(.) p=c(LENGTH)
S(.) γ(.) p=c(.)
S(.) γ(Markovian(LENGTH)) p=c(.)
S(.) γ(Markovian(LENGTH)) p=c(LENGTH)
S(.) γ(Markovian) p=c(.)
S(.) γ(Markovian) p=c(LENGTH)
S(.) γ(No Movement) p=c(.)
S(.) γ(No Movement) p=c(LENGTH)
S(.) γ(Random(LENGTH)) p=c(.)
S(.) γ(Random(LENGTH)) p=c(LENGTH)
S(.) γ(Random) p=c(.)
S(.) γ(Random) p=c(LENGTH)
S(.) γ(t+LENGTH) p=c(.)
S(.) γ(t+LENGTH) p=c(LENGTH)
S(t) γ(.) p=c(.)
S(t) γ(.) p=c(LENGTH)
S(t) γ(LENGTH) p=c(.)
S(t) γ(LENGTH) p=c(LENGTH)
S(t) γ(Markovian(LENGTH)) p=c(.)
S(t) γ(Markovian(LENGTH)) p=c(LENGTH)
S(t) γ(Markovian) p=c(.)
S(t) γ(Markovian) p=c(LENGTH)
S(t) γ(No Movement) p=c(.)
S(t) γ(No Movement) p=c(LENGTH)
S(t) γ(Random(LENGTH)) p=c(.)
S(t) γ(Random(LENGTH)) p=c(LENGTH)
S(t) γ(Random) p=c(.)
S(t) γ(Random) p=c(LENGTH)

Table S.3. Full candidate model set for the within year closed capture abundance estimates. Models include initial detection probability (*p*), and subsequent detection probability (*c)* as parameters. For each parameter, "*t*" represents time variation and "." indicates that the parameter was held constant. Both time varying and constant models may be modeled as functions of the *LENGTH* covariates. Additive models are represented by a "+" symbol.

Model Name
p(.(LENGTH)) c(.(LENGTH)
p(.(LENGTH+LENGTH^2)) c(.(LENGTH+LENGTH^2)
p(.) c(.)
p(Markovian) c(t) [p_i=c_i]
p(Markovian) c(t) [p_i=p_{i-1}]
p(t(LENGTH)) c(t(LENGTH))
p(t(LENGTH+LENGTH2)) c(t(LENGTH+LENGTH^2))
p=c(.)
p=c(.(LENGTH))
p=c(.(LENGTH+LENGTH^2))
p=c(t(LENGTH))
p=c(t(LENGTH+LENGTH^2))
p=c(t)

Table S.4. Candidate model set for the Robust Design analysis (Huggins) for East and Panther Lakes. Models include Survival (*S*), initial detection probability (*p*), and subsequent detection probability (*c*). The "no movement" γ parameterization was used exclusively in this analysis and is not shown (see explanation in text).

Model Name
S(.) p=c(.)
S(.) p=c(LENGTH)
S(.) p=c(LENGTH+LENGTH^2)
S(t) p=c(.)
S(t) p=c(LENGTH)
S(t) p=c(LENGTH+LENGTH^2)
S(LENGTH) p=c(LENGTH)
S(LENGTH) p=c(LENGTH+LENGTH^2)
S(LENGTH+LENGTH^2) p=c(LENGTH)
S(LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)
S(DD18) p=c(.)
S(DD18) p=c(LENGTH)
S(DD18) p=c(LENGTH+LENGTH^2)
S(DD18+LENGTH) p=c(.)
S(DD18+LENGTH) p=c(LENGTH)
S(DD18+LENGTH) p=c(LENGTH+LENGTH^2)
S(DD18+LENGTH+LENGTH^2) p=c(.)
S(DD18+LENGTH+LENGTH^2) p=c(LENGTH)
S(DD18+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)
S(DD19) p=c(.)
S(DD19) p=c(LENGTH)
S(DD19) p=c(LENGTH+LENGTH^2)
S(DD19+LENGTH) p=c(.)
S(DD19+LENGTH) p=c(LENGTH)
S(DD19+LENGTH) p=c(LENGTH+LENGTH^2)
S(DD19+LENGTH+LENGTH^2) p=c(.)
S(DD19 +LENGTH+LENGTH^2) p=c(LENGTH)
S(DD19+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)
S(DD20) p=c(.)
S(DD20) p=c(.)
S(DD20) p=c(LENGTH)
S(DD20) p=c(LENGTH+LENGTH^2)
S(DD20+LENGTH) p=c(LENGTH)
S(DD20+LENGTH) p=c(LENGTH+LENGTH^2)
S(DD20+LENGTH+LENGTH^2) p=c(.)
S(DD20+LENGTH+LENGTH^2) p=c(LENGTH)

Table S.4 (continued).

S(DD20+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)
S(DD21) p=c(.)
S(DD21) p=c(.)
S(DD21) p=c(LENGTH)
S(DD21) p=c(LENGTH+LENGTH^2)
S(DD21+LENGTH) p=c(LENGTH)
S(DD21+LENGTH) p=c(LENGTH+LENGTH^2)
S(DD21+LENGTH+LENGTH^2) p=c(.)
S(DD21+LENGTH+LENGTH^2) p=c(LENGTH)
S(DD21+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)
S(DD22) p=c(.)
S(DD22) p=c(LENGTH)
S(DD22) p=c(LENGTH+LENGTH^2)
S(DD22+LENGTH) p=c(.)
S(DD22+LENGTH) p=c(LENGTH)
S(DD22+LENGTH) p=c(LENGTH+LENGTH^2)
S(DD22+LENGTH+LENGTH^2) p=c(.)
S(DD22+LENGTH+LENGTH^2) p=c(LENGTH)
S(DD22+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)
S(MAXTEMP) p=c(.)
S(MAXTEMP) p=c(LENGTH)
S(MAXTEMP) p=c(LENGTH+LENGTH^2)
S(MAXTEMP+LENGTH) p=c(.)
S(MAXTEMP+LENGTH) p=c(LENGTH)
S(MAXTEMP+LENGTH) p=c(LENGTH+LENGTH^2)
S(MAXTEMP+LENGTH+LENGTH^2) p=c(.)
S(MAXTEMP+LENGTH+LENGTH^2) p=c(LENGTH)
S(MAXTEMP+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)
S(WINTEMP) p=c(.)
S(WINTEMP) p=c(LENGTH)
S(WINTEMP) p=c(LENGTH+LENGTH^2)
S(WINTEMP+LENGTH) p=c(.)
S(WINTEMP+LENGTH) p=c(LENGTH)
S(WINTEMP+LENGTH) p=c(LENGTH+LENGTH^2)
S(WINTEMP+LENGTH+LENGTH^2) p=c(.)
S(WINTEMP+LENGTH+LENGTH^2) p=c(LENGTH)
S(WINTEMP+LENGTH+LENGTH^2) p=c(LENGTH+LENGTH^2)

Table S.5. Candidate model set for the Robust Design analysis (Huggins) for Wilmurt Lake. Models include Survival (*S*), initial detection probability (*p*), and subsequent detection probability (*c*). The "no movement" γ parameterization was used exclusively in this analysis and is not shown (see explanation in text).

Model
S(.) p(.(LENGTH+LENGTH^2) c(.(LENGTH+LENGTH^2))
S(.) p(.(LENGTH+LENGTH^2)) c(.)
S(.) p(.(LENGTHLENGTH^2)) c(t)
S(.) p(t(LENGTH+LENGTH^2)) c(.)
S(.) p(.(LENGTH+p LENGTH^2)) c(t(LENGTH+LENGTH^2))
S(.) p(.) c(.)
S(.) p(.) c(t)
S(.) p(MARK) c(.)
S(.) p(MARK) c(t)
S(.) p(t(LENGTH+LENGTH^2) c(.(LENGTH+LENGTH^2))
S(.) p(t(LENGTH+LENGTH^2) c(t(LENGTH+LENGTH^2))
S(.) p(t(LENGTH+LENGTH^2)) c(t)
S(LENGTH+LENGTH^2) c(t)
S(LENGTH+LENGTH^2) p(.(LENGTH+LENGTH^2) c(.(LENGTH+LENGTH^2))
S(LENGTH+LENGTH^2) p(.(LENGTH+LENGTH^2) c(.)
S(LENGTH+LENGTH^2) p(.(LENGTH+LENGTH^2) c(t(LENGTH+LENGTH^2)
S(LENGTH+LENGTH^2) p(.(LENGTH+LENGTH^2)) c(t)
S(LENGTH+LENGTH^2) p(.) c(.)
S(LENGTH+LENGTH^2) p(MARK) (c.(LENGTH+LENGTH^2))
S(LENGTH+LENGTH^2) p(MARK) c(.)
S(LENGTH+LENGTH^2) p(MARK) c(t)
S(LENGTH+LENGTH^2) p(t(LENGTH+LENGTH^2) c(.(LENGTH+LENGTH^2))
S(LENGTH+LENGTH^2) p(t(LENGTH+LENGTH^2) c(t(LENGTH+LENGTH^2))
S(LENGTH+LENGTH^2) p(t(LENGTH+LENGTH^2) c(t)
S(LENGTH+LENGTH^2) p(t(LENGTH+LENGTH^2)) c(.)
S(LENGTH+LENGTH^2) p=c(.(LENGTH+LENGTH^2))
S(LENGTH+LENGTH^2) p=c(.)
S(LENGTH+LENGTH^2) p=c(t(LENGTH+LENGTH^2))
S(LENGTH+LENGTH^2) p=c(t)
S(t) p(.) c(.)
S(t) p(.(LENGTH+LENGTH^2) c(t(LENGTH+LENGTH^2))
S(t) p(.(LENGTH+LENGTH^2)) c(.(LENGTH+LENGTH^2))
S(t) p(.(LENGTH+LENGTH^2)) c(.)

Table S.5 (continued).

S(t) p(.(LENGTH+LENGTH^2)) c(t)
S(t) p(.) c(t)
S(t) p(MARK) c(.)
S(t) p(MARK) c(t)
S(t) p(t(LENGTH+LENGTH^2)) c(.(LENGTH+LENGTH^2))
S(t) p(t(LENGTH+LENGTH^2)) c(.)
S(t) p(t(LENGTH+LENGTH^2)) c(t(LENGTH+LENGTH^2))
S(t) p(t(LENGTH+LENGTH^2)) c(t)
S(t) p=c(.(LENGTH+LENGTH^2))
s(t) p=c(.)
S(t) p=c(t(LENGTH+LENGTH^2))
S(t) p=c(t)

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